SWIMMING ENDURANCE OF AMERICAN PLAICE (Hippoglossoides platessoides) AND ATLANTIC COD (Gadus morhua): IMPLICATIONS FOR CATCHABILITY BY OTTER TRAWLS

PAUL D. WINGER

Swimming endurance of American plaice *(Hippoglossoides platessoides)* and Atlantic cod (*Gadus morhua*): implications for catchability by otter trawls

by

© Paul D. Winger

A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

Biopsychology Programme

Memorial University of Newfoundland

St. John's, Newfoundland, Canada

1998

Abstract

Identifying and measuring the factors that affect the catchability of otter trawl fishing gear has been the subject of much research in recent years. Variation in catching efficiency is known to be associated with changes in the vulnerability of fish to trawl capture. In particular, the swimming capability of fish in response to an approaching trawl plays an important role in determining the likelihood of successful capture. In order to quantify the efficiency of the capture process, knowledge of the swimming endurance of marine groundfish species is necessary. The purpose of this study was to investigate factors affecting the swimming endurance of American plaice (*Hippoglossoides platessoides*) and Atlantic cod (*Gadus morhua*) under laboratory conditions. The effects of fish length, water temperature and swimming speed were examined using a swimming flume. The data were analyzed using failure time (survival) analysis, a more robust statistical technique for endurance-type data when censored observations require consideration.

Swimming trials for plaice were conducted across a range of fish lengths (14 to 44 cm) and water temperatures (-0.2 to 9.7 C) at a swimming speed of 0.30 m/s. The probability of plaice achieving a given endurance was found to significantly improve with increasing fish length and water temperature. The findings indicate that the herding of plaice by otter trawl sweeps may be size- and temperature-dependent. At low temperatures, small plaice are expected to have a lower probability of sufficient

endurance required to reach the path of an approaching trawl, thereby experience a greater likelihood of escaping capture.

Swimming trials for cod were conducted across a range of fish lengths (41 to 86 cm), water temperatures (0.0 to 9.8 C) and swimming speeds (0.60 to 1.30 m/s). Swimming speed was the only factor found to significantly affect the endurance of cod. The probability of achieving a given endurance was found to decrease rapidly with increasing swimming speed. The findings indicate that even small changes in the speed of a trawl through the water could dramatically affect the rate of exhaustion, i.e. turn-over rate, of cod swimming in the mouth of a trawl.

Acknowledgements

This project was funded through the Department of Fisheries and Oceans (DFO) ADM Strategic Science Project # 90040 and by The Fishing Technology Unit of the Fisheries and Marine Institute of Memorial University of Newfoundland.

I am indebted to many individuals for their support. In particular, I am grateful to my supervisor, Pingguo He, who has been a continual source of wisdom and enthusiasm for me throughout this research. Other members of my supervisory committee included Stephen Walsh and Bill Montevecchi whose continuing support, advice and review comments on early drafts of the thesis/papers have proven invaluable. Several other individuals deserve recognition for their logistical support. I thank George Legge for his electrical and mechanical assistance with the operation and maintenance of the swimming flume. Special thanks is also given to Ross Wilson, Jim Devereaux and the many members of the Ocean Sciences Centre's facilities management staff. Appreciation is given to several individuals within the DFO Groundfish Division for the collection and care of live fish, including Dave Orr, Mick Veitch and Paul Higdon. Finally, I am thankful to Noel Cadigan for statistical consultation.

Of greatest importance, I give special recognition to my loving wife, Jennifer. Without her support and encouragement, the many tedious hours of laboratory testing could not have been possible.

Table of Contents

List of Tables

List of Figures

Chapter 1. Introduction

1.1 Fish behaviour near otter trawls

In the Northwest Atlantic, commercial groundfish species are most commonly harvested using otter trawls. This is an active (or mobile) type of fishing gear that is towed along the bottom of the ocean (Figure 1.1). The interaction between fish and otter trawls has received increasing attention since the early 1950's. It is now well established that otter trawls do not capture fish by mere passive filtering of the water. Instead, the process of fish capture involves a complex sequence of fish behaviour in response to the fishing vessel and the various components of the trawl. These behaviour patterns are generally avoidance responses to the visual and auditory stimuli produced by the vessel, doors, sand clouds, sweeps, footgear and trawl netting.

The average proportion of fish that are effectively captured per unit of fishing effort is defined as the *catchability* of a trawl (Gunderson, 1993). Godø (1994) and Walsh (1996) have described three zones during the fish capture process in which fish behaviour can influence otter trawl catchability (Figure 1.2). The process begins ahead of the doors (*zone 1*) where vessel avoidance behaviour can first occur. Low frequency noise associated with propeller cavitation has been shown to induce avoidance behaviour in certain species well before the trawl can be seen or heard. Ona and Godø (1990) have shown that Atlantic cod (*Gadus morhua*) will dive toward the seafloor in response to vessel noise. This results in a compression of the vertical distribution of the fish

aggregation and can increase the number of fish available to be captured by the approaching trawl. By comparison, the available data for flatfish species has indicated that very little avoidance behaviour occurs in response to vessel noise. Harden Jones et al. (1977) reported that North Sea plaice (*Pleuronectes platessa*) equipped with acoustic transponding tags showed little avoidance behaviour until within 1-2 m of direct collision with the doors of a trawl.

As the trawl begins to move through an aggregation of fish, a proportion of these fish will enter between the doors (*zone 2*). The herding behaviour of fish toward the trawl mouth is again species-specific. For roundfish, the general behaviour has been described as a 'fountain manoeuvre' (Wardle, 1993). In general, fish appear to avoid an approaching door by swimming either to the left or right while maintaining at least one eye on the door at all times. Those fish which swim to the inside of the doors tend to immediately enter the trawl path and begin swimming gently toward the trawl mouth maintaining position equidistant between the sweeps and sand clouds. For flatfish, many will lie initially in the trawl path while others will lie in the sweep zone between the wings and doors (Figure 1.2). Flatfish that occur in the latter can be effectively herded into the trawl path following direct or near contact with the doors, sweeps and sand clouds. Once disturbed from the seafloor, the distance required to swim in order to reach the trawl path is a function of a) the sweep angle, b) the position along the sweep where the fish initially encounters the gear, and c) the angle of avoidance in which the fish

chooses to swim (Foster et al., 1981).

Fish which eventually arrive at the mouth of the trawl will tend to orient in the direction of tow and keep station with the advancing trawl for a varying period of time depending on their individual endurance. This is true for both roundfish and flatfish species. This behaviour appears to be an optomotor reflex in response to the visual cues produced by the surrounding footgear and/or netting of the trawl wings (Wardle, 1993). As the fish begin to exhaust, the majority will turn and fall back into the trawl (*zone 3*), but some may effectively escape over the headline (Main and Sangster, 1981) or under the footgear (Engås and Godø, 1989b; Godø and Walsh, 1992; Walsh, 1992). Once inside the trawl, mesh selection can still occur. Depending on the design of the codend, mesh size, and mesh shape, a significant number of juvenile fish may still escape from capture (e.g. Robertson, 1989; Walsh et al., 1992).

Identifying and measuring the factors that affect otter trawl catchability has been the subject of much research in recent years (e.g. Byrne et al., 1981; Engås and Godø, 1989a, 1989b; Godø and Walsh, 1992; Godø, 1994; Walsh, 1996). Variation in catching efficiency is known to be associated with changes in the *vulnerability* of fish to trawl capture. Vulnerability refers to the likelihood of an individual fish being captured once it is in contact with the fishing gear. Whether a fish is successful in avoiding capture is thought to be related to its swimming capability, including its maximum swimming speed, maneuverability and swimming endurance. Factors suspected of affecting

swimming capability and hence avoidance success include fish size, age, physiological condition, ambient light intensity and bottom temperature (e.g. Parrish et al., 1964; Foster et al., 1981; Wardle, 1983, 1993; Glass and Wardle, 1989; He, 1991, 1993; Walsh, 1991; Walsh and Hickey, 1993). As a result, not all species and sizes of fish are captured with equal probability across all environmental conditions. Research relating to the swimming capability of marine groundfish species is therefore necessary in order to better understand the factors that may affect their vulnerability to capture by otter trawls. Of major interest is the swimming endurance of different commercially exploited species of different sizes across a range of swimming speeds and water temperatures. This knowledge will become critical in future attempts to quantify the efficiency of the capture process of both commercial and research survey trawls.

1.2 Swimming Speed and Endurance

A number of laboratory studies have examined the swimming speed and endurance of fish in the past few decades. Several types of swimming chambers have been designed to achieve this objective, including fish wheels (Bainbridge, 1960), large annular tanks (He and Wardle, 1986, 1988) and swimming flumes (e.g. Beamish, 1966, 1984; Brett, 1964, 1967; He, 1991). The experimental approach of these studies has typically involved measuring the time to fatigue, i.e. endurance, across a range of fixed swimming speeds. A useful classification for describing endurance at different

swimming speeds was introduced by Hoar and Randall (1978). This includes three major categories of swimming speeds: *sustained*, *prolonged* and *burst* (for review see He, 1993). The slowest range of speeds is the sustained swimming speeds. Here, swimming is predominantly driven by the slow-twitch (red) aerobic musculature of the fish. Oxygen debt does not occur at these speeds and fish are capable of swimming for very long periods without showing signs of fatigue. One of the most impressive examples was reported by Beamish (1966) who successfully encouraged redfish (*Sebastes marinus*) to swim for more than seven days at 0.45 m/s. The upper limit of the sustained swimming speeds is called the maximum sustained swimming speed (U_{ms}). This is defined as the maximum swimming speed for which a minimum endurance of 200 min can be maintained. Speeds exceeding the U_{ms} are referred to as the prolonged swimming speeds. Fast-twitch (white) muscle fibers are increasingly recruited at prolonged swimming speeds in order to provide sufficient mechanical power. Endurance is limited at these speeds due to increasing lactate concentrations and declining glycogen reserves. The upper limit of the prolonged swimming speeds is called the maximum prolonged swimming speed (U_{mp}). This is defined as the maximum swimming speed for which a minimum endurance of 15-20 s can be maintained. Speeds exceeding the U_{mp} are referred to as burst swimming speeds. Only the fast-twitch (white) musculature of the fish effectively contributes to the required mechanical power at burst swimming speeds and endurance never lasts more than a few seconds before fatiguing.

The relationship between endurance and swimming speed (body lengths per second; BL/s) has traditionally been modelled using regression analysis (Figure 1.3). Separate regression lines are produced for each of the prolonged and burst swimming speed ranges since they are often characterized by different slopes (Brett, 1964). Specifically, endurance within the range of prolonged speeds tends to decline more rapidly with increasing swimming speed than compared to burst speeds. The points of inflection of the resulting 'endurance curve' define both the U_{ms} and the U_{mp}. These values and the slopes of the endurance curve have been the most commonly used parameters for the comparison of endurance data across species and experimental treatments (e.g. Videler and Wardle, 1991). Previous studies have shown that endurance can vary across species, swimming speed, fish size and water temperature (e.g. Bainbridge, 1960; Brett, 1964, 1967; Beamish, 1966; He and Wardle, 1988; Wardle and He, 1988; He 1991).

1.3 Study objectives

The objective of this study was to examine potential factors affecting the catchability of American plaice (*Hippoglossoides platessoides*) and Atlantic cod (*Gadus morhua*) by otter trawls. To meet this objective, laboratory experiments investigating the swimming capability of these species were proposed. This involved measuring the endurance of experimental specimens under laboratory conditions using a large

swimming flume. Particular factors of interest included fish length, water temperature and swimming speed. Pilot trials were conducted in October of 1996 to determine the feasibility of the study and to develop an experimental methodology. Based on the findings of the pilot study, it became apparent that separate experiments would need to be conducted for each species.

A) Assess the swimming endurance of American plaice:

The results of the pilot study revealed that plaice of different fish lengths could be induced to swim at various water temperatures, but only within a very limited range of swimming speeds. Most of the fish were found to swim comfortably and reliably only at swimming speeds less than or equal to 0.30 m/s. This range of speeds falls within the approximate range of swimming speeds required during the herding process of otter trawls, but does not nearly approach the swimming speeds required while swimming in a trawl mouth. Hence, the objective of this experiment (Chapter Three) was to examine the effects of fish length and water temperature on the endurance of plaice at swimming speeds comparable to the herding speeds of trawl sweeps. The implications for trawl catchability are discussed in Chapter Five.

B) Assess the swimming endurance of Atlantic cod:

The results of the pilot study revealed that cod of different fish lengths could be

induced to swim with relative ease at various water temperatures and swimming speeds. The most effective speeds for measuring the endurance of cod were found to lie between 0.60 and 1.30 m/s. This range of speeds is comparable to the faster swimming speeds required while swimming in a trawl mouth, but is well above those expected during the herding of sweeps. Hence, the objective of this experiment (Chapter Four) was to examine the effects of fish length and water temperature on the endurance of cod at swimming speeds comparable to those required when swimming in a trawl mouth. The implications for trawl catchability are also discussed in Chapter Five.

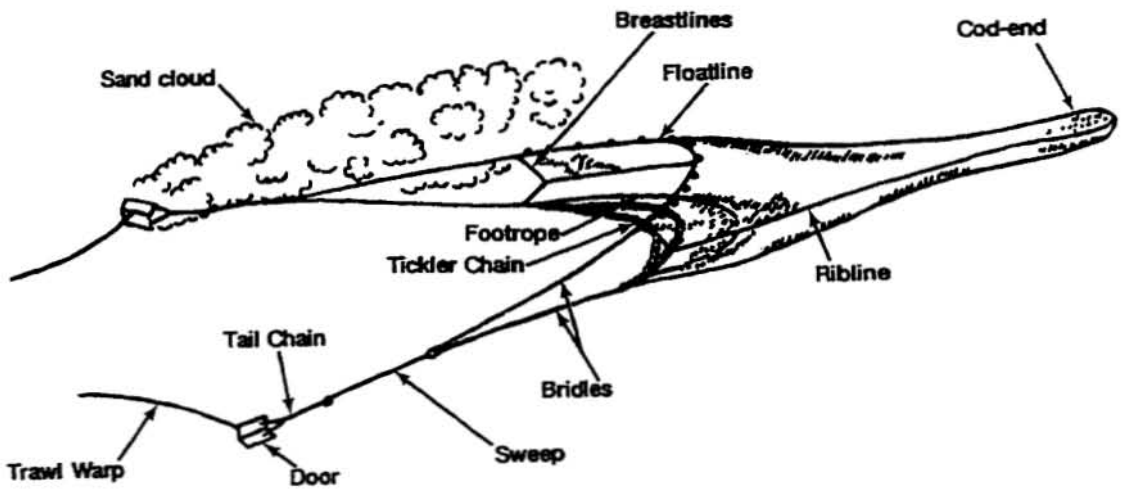

Figure 1.1. Schematic drawing of an otter trawl (Adapted from Gunderson, 1993).

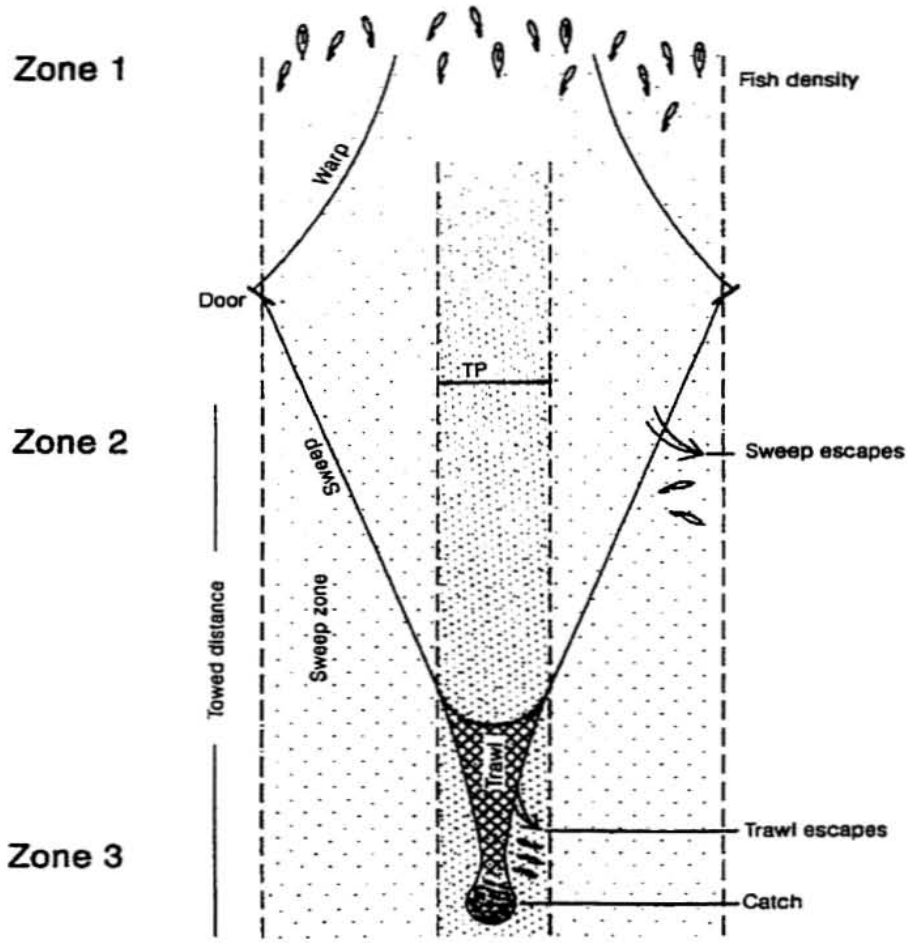

Figure 1.2. The three catching zones of influence in the fish capture process. TP = trawl path. (Adopted from Godø, 1994; Walsh, 1996).

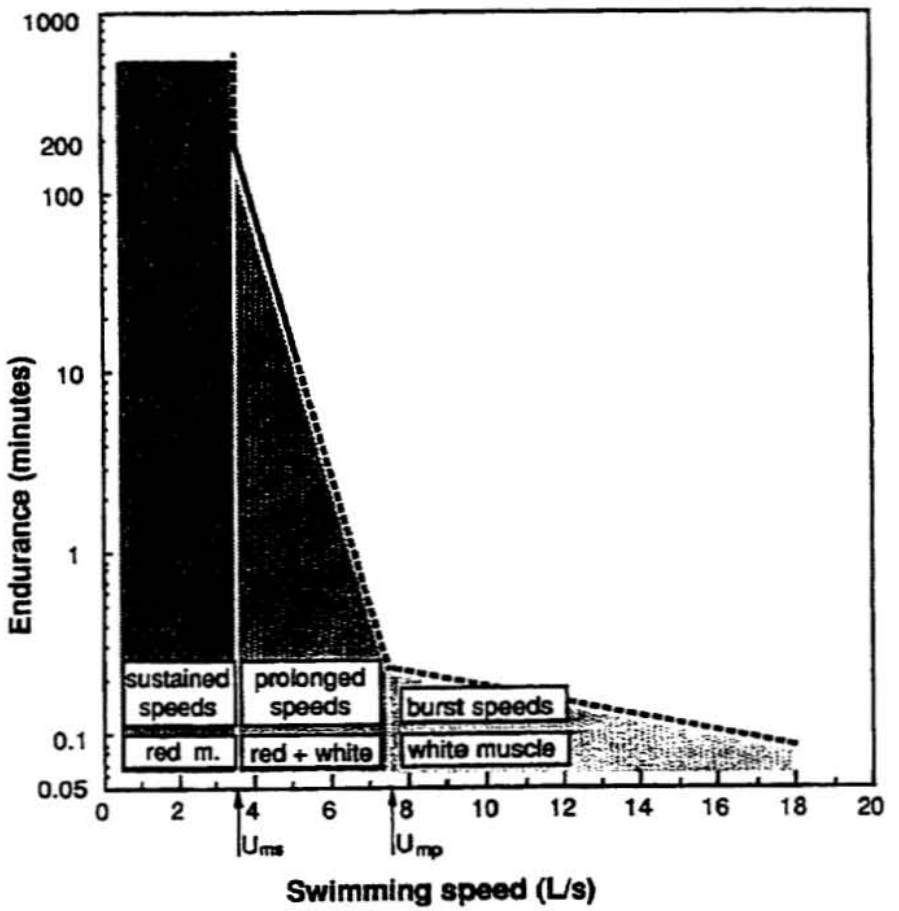

Figure 1.3. Typical endurance curve outlining the sustained, prolonged and burst swimming speed ranges and the different types of muscles used within these ranges. The points of inflection on the curve define both the U_{ms} and the U_{mp} performance thresholds. Data shown are for Atlantic mackerel (*Scomber scombrus*) (Adapted from He, 1993).

Chapter 2. General Methodology

2.1 Specimens

Cod and plaice were captured at several times throughout 1996-97 to support the experiments (Table 2.1). The fish were transported to the Ocean Sciences Centre of Memorial University of Newfoundland for tank adaptation and endurance testing. Cod were kept in a large raceway compartment with dimensions 2.5 x 2.5 x 1.0 m while the plaice were kept in a smaller 2.0 x 2.0 x 0.5 m fiberglass tank. Both tanks received a continuous supply of fresh ambient temperature seawater. The indoor lighting was operated using an outdoor light sensor thereby synchronizing the photoperiod with seasonal changes in day length. The fish were fed a diet of chopped Atlantic herring (*Clupea harengus*) once a week to satiation. All fish were starved for a minimum period of 48 h prior to endurance testing. Only fish that appeared in good condition were used. Fish were excluded if they showed visible signs of a) weight loss or b) epidermal haemorrhaging and/or scarring. A minimum duration of three weeks was permitted for tank adaptation before endurance testing.

2.2 Apparatus

The swimming flume used in this study is the largest of its kind, with a total water volume of 3450 L (Figures 2.1 and 2.2). The swimming chamber has a maximum working area of 2.5 x 1.0 x 0.5 m (length x width x depth). Adjustable plexiglass panels

can be inserted inside the chamber in order to customize the width. The length of the chamber can also be adjusted by repositioning either of the upstream or downstream screens. Three electric 1-hp pumps deliver a continuous water flow. The maximum speed of flow within the chamber can be increased by reducing the chamber width and/or water depth. The floor of the swimming chamber is equipped with a moving belt. The belt moves in the direction of the water flow and can be adjusted to match the speed of flow up to a maximum of 1.00 m/s. This continuously moving belt serves several purposes: a) preventing negatively buoyant fish, such as flatfish, from adhering to the floor of the chamber, b) simulating ground passing under a swimming fish as it would appear in the ocean, and c) maintaining uniformity of flow near the floor of the chamber thus preventing fish from taking advantage of reduced flow in that area. Vertical black bars presented on the walls of the chamber provide fish with a visual cue and encourage forward swimming into the water current (Beamish, 1978). Pairs of stainless steel electrodes installed in the downstream end of the chamber provide a pulsing electrical stimulus (DC voltage) which also encourages swimming. A floating plexiglass cover can be positioned on the water surface to reduce turbulence and improve uniformity of flow within the chamber. Specific modifications to the apparatus for each of the experiments are described separately in Chapter Three for plaice and Chapter Four for cod. For further description of the swimming flume see He (1991).

The swimming flume was operated on a flow-through basis with a continuous

supply of fresh coastal seawater. Seasonal changes in the ambient temperature of incoming seawater provided the opportunity to test for temperature-dependent effects on swimming endurance. Auxiliary holding tanks were established near the flume for additional acclimation and recovery of fish. Measures of water temperature, dissolved oxygen content, and oxygen saturation were recorded for all swimming trials using a portable digital meter (Model UK-2000, Central Kagaku Corp.). Calibration of flow speeds was conducted using a Seba mini-current meter (Model 486, Geneq Inc.).

2.3 Measuring Endurance

Swimming endurance was defined as the period of time a fish was able to swim at a target speed before becoming exhausted. A fish was considered exhausted when it was unable to lift-off the downstream screen after a duration of 10 s. Swimming was encouraged by emitting a continuously pulsing electrical stimulus from the downstream electrodes. Details on the frequency and voltage of electricity emitted are described in Chapter Three for plaice and Chapter Four for cod. The selection of appropriate electrical stimuli was based on initial pilot trials for each species and from the established guidelines for swimming related studies (Bell and Terhune, 1970; Beamish, 1978). Prodding techniques used in similar studies (e.g. Beamish, 1966; Taylor and McPhail, 1985) were not used in order to avoid the possibility of subjectively biasing the results. In cases where endurance exceeded 200 min, the trials were terminated and the data were

treated as *censored* observations (see Section 2.4, Statistical Analysis). In these cases, exhaustion was not observed and the total time to fatigue was therefore not known. Data of this nature are common among endurance studies (Brett, 1964, 1967; Beamish, 1966; He and Wardle, 1988; He, 1991) in which fish (under certain conditions) fail to exhaust within an appreciable period of time and the experimenter must eventually terminate the trial. The 200 min cut-off period used in this study was chosen a priori and is consistent with the methodology of He and Wardle (1988) and He (1991).

Given the limited numbers of fish and tank space available, endurance testing of the same fish a number of times was necessary for suitable replication. Experimental fish were selected from the holding tanks haphazardly without replacement in order to optimize the recovery period before retesting any given fish again. The minimum recovery period was generally one week. With the arrival of new fish (Table 2.1), it was estimated that the maximum number of trials for any given fish did not exceed four.

2.4 Statistical Analysis

Measures of swimming endurance are by definition classified as *time-to-event* data. Modelling this type of data as a function of one or more independent variables has traditionally been done using regression analysis as discussed in Chapter One (for reviews see Beamish, 1978; Videler, 1993). The disadvantage of this technique, however, is that it cannot accommodate censored observations. As a result, previous

endurance studies have typically excluded censored swimming trials from their analyses entirely or simply discussed them in a qualitative manner (e.g. Brett, 1964, 1967; Beamish, 1966; He and Wardle, 1988; He, 1991). It is argued here that endurance data cannot be appropriately analyzed by simply excluding censored observations for ease of analysis. A major problem with this approach is the fact that censoring is often more likely to occur under certain experimental conditions than others. In fact, it is expected that fish of larger length swimming at warmer water temperatures and slower swimming speeds will experience a greater likelihood of being censored. Excluding this portion of the dataset could potentially bias the analysis and conclusions. Clearly, the appropriate method of analysis must accommodate both the uncensored observations as well as the censored observations.

An analysis of the endurance data for plaice and cod was conducted using a relatively new and alternative statistical technique referred to as failure time analysis, or survival analysis. Unlike regression analysis, this technique is designed specifically for time-to-event data (see discussions by: Muenchow, 1986; Lee, 1992; Marubini and Valsecchi, 1995). This type of data is unique for several reasons: a) the distribution of failure (endurance) times are often skewed or far from normal, b) failure time is a non-negative random variable assuming values in the interval from zero to T, and c) the dataset often contains censored observations. Perhaps the primary advantage of this technique over traditional regression analysis is that it can accommodate censored

observations. Therefore, even those fish which did not exhaust within 200 min, for example, can be included in this type of analysis.

The purpose of failure time analysis is to model the underlying distribution of failure time (T) and to assess the dependence of T on independent predictor variables. The probability distribution of T can be specified several ways, although two are particularly useful in failure time analysis. This includes the *survivorship* function and the *hazard* function. The survivorship function, $S(t)$, is the probability that an individual survives (i.e. has endurance) longer than time t. It can also be interpreted as the proportion of individuals still surviving at time t. By comparison, the hazard function, $h(t)$, is the conditional failure rate or instantaneous failure rate at time t. It is a measure of the proneness to failure as a function of the independent predictor variables.

In the current study, the distribution of endurance time (T) for plaice and cod is modelled using the Cox Proportional Hazards Model (Cox, 1972; Cox and Oakes, 1984). This is a semi-generalized linear model analogous to multiple regression analysis. An important distinction, however, is that the dependent variable being modelled is not endurance per se, but the instantaneous rate of exhaustion, or *hazard rate* at time t. The hazard function is expressed as a function of time and one or more independent predictor variables. The general form of the hazard function is given by:

$$h(t) = h_0(t)\ e^{\beta x}$$

where βX represents the regression function, $\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p$, and $h_0(t)$ is the time dependent baseline hazard function. In this model, the independent variables (X_i) act multiplicatively on the hazard function. The regression coefficients (β_i) are derived using the method of partial likelihood (Kalbfleisch and Prentice, 1980). If the regression coefficients (β_i) are all equal to zero (i.e. the independent variables have no effect on endurance), then the exponent term $e^{\beta X}$ equals one, and the hazard function $h(t)$ is equal to the baseline hazard function $h_0(t)$. If the coefficients are different from zero, then $e^{\beta X}$ is positive and the hazard function is some multiple of the baseline hazard function. The model is referred to as a *proportional hazards* model since the hazards remain in the same proportion for all t for any given set of values of the independent variables.

The proportional hazards models for plaice and cod were developed using forward stepwise variable selection analogous to multiple regression analysis. The order of entry of the variables into the model was based on their level of significance of the Score statistic (Norušis, 1994). A variable was entered if its p-value was less than $\alpha = 0.05$. After a variable was added to the model, all variables already in the model were examined for removal. Criteria for removal from the model was based on a variable's level of contribution to the reduction of the log-likelihood value for the model (likelihood ratio test; Lee, 1992). A variable was removed if its p-value was greater than $\alpha = 0.10$. All independent variables were treated as continuous variables. Diagnostic methods for the examination of the dataset were conducted by investigating the DfBeta plots and

partial residual plots. The assumption of proportional hazards (between individuals across time) was checked by plotting the log of the negative of the log of the cumulative survival function against swimming endurance (Norušis, 1994), also known as log-minus-log plots. All analyses were carried out using SPSS version 6.1.

Table 2.1. A listing of the capture dates, locations and gear types used for the aquisition of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) to support the experiment.

Date	Species	Location of Capture	Gear Type
Jun. 27 1996	cod & plaice	Grand Bank	otter trawl
Aug. 14 1996	cod	Petty Harbour, Nfld.	cod trap
Nov. 7 1996	cod	Sugarloaf Point, Nfld.	handline
Nov. 22 1996	plaice	Grand Bank	otter trawl
Nov. 23 1996	plaice	Grand Bank	otter trawl
Nov. 25 1996	plaice	Grand Bank	otter trawl
Dec. 7 1996	plaice	Grand Bank	otter trawl
Feb. 20 1997	cod	Northwest Arm, Trinity Bay, Nfld.	handline
Mar. 18 1997	cod	Smith Sound, Trinity Bay, Nfld.	longline
Mar. 20 1997	cod	Smith Sound, Trinity Bay, Nfld.	longline
Mar. 21 1997	cod	Smith Sound, Trinity Bay, Nfld.	longline
Apr. 25 1997	cod & plaice	St. Pierre Bank	otter trawl
May 9 1997	plaice	Grand Bank	otter trawl
Jun. 9 1997	cod	Fox Harbour, Nfld.	cod trap

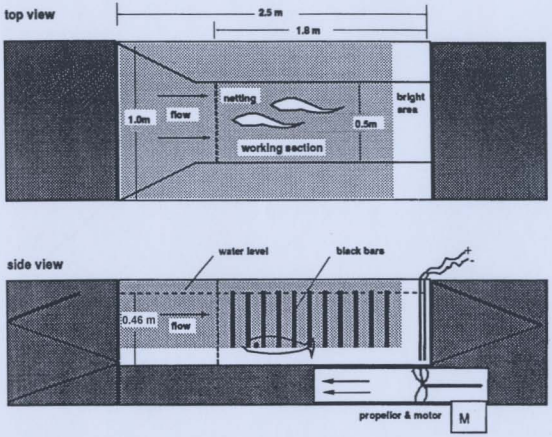

Figure 2.1. Schematic drawing of the swimming flume used to test the endurance of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*). Not drawn to scale. (Adapted from He, 1991).

Figure 2.2. View of the swimming flume used for endurance testing owned by the Fisheries and Marine Institute of Memorial University of Newfoundland. Shown is a 53 cm Atlantic cod (*Gadus morhua*) swimming at 0.60 m/s.

Chapter 3. Swimming Endurance of American Plaice

3.1 Introduction

The primary literature on the swimming performance of flatfish species is limited to only a few studies. Much of the research has concentrated on measuring maximum or critical swimming speeds (U_{crit}) with little attention to swimming endurance at fixed speeds. Blaxter and Dickson (1959) observed an increasing trend in the maximum swimming speeds of North Sea plaice (*Pleuronectes platessa*) with increasing water temperature and fish length. For this same species, Priede and Holliday (1980) reported an increasing trend in U_{crit} values with increasing temperature. Similar findings were also found for European flounder (*Platichthys flesus*), but could not be demonstrated for common dab (*Limanda limanda*) or lemon sole (*Microstomus kitt*) (Duthie, 1982). The only previously known study which has directly investigated the swimming endurance of flatfish was by Beamish (1966). In that study, winter flounder (*Pleuronectes americanus*) (19 - 23 cm) were tested at temperatures of 5.0, 8.0, 11.0 and 14.0 C and at swimming speeds ranging from 0.75 to 1.35 m/s. Beamish (1966) did observe increased levels of endurance at 14.0 C, but found no appreciable difference in swimming endurance across the lower temperature treatments. Other quantitative endurance data for flatfish of different sizes, at low temperatures and at low swimming speeds is lacking.

The purpose of this experiment was to investigate factors affecting the swimming endurance of American plaice. No laboratory studies have previously evaluated the

swimming capability of this species. Two hypotheses were tested: a) endurance will increase with increasing fish length, and b) endurance will increase with increasing water temperature. The results are discussed in relation to other flatfish swimming studies, and in Chapter Five the data are used to illustrate the implications for trawl catchability.

3.2 Materials and Methods

Endurance trials were completed over a duration of 16 weeks during the months of February to June of 1997. This experiment was conducted concurrently with the Atlantic cod experiment which will be described in Chapter Four. Measures of endurance were recorded for plaice ranging in length from 14 to 44 cm ($\bar{x}$ = 30.8 cm, s.d. = 6.9). Trials were conducted opportunistically at water temperatures ranging from -0.2 to 9.7 C ($\bar{x}$ = 3.4 C, s.d. = 2.8) as the ambient temperature of incoming coastal seawater changed across seasons.

Pilot trials were conducted in October of 1996 to determine which experimental flume conditions would best encourage plaice to swim. The maximum chamber size and water depth proved inefficient since the fish tended to either turn around frequently or flare-up perpendicular to the direction of water flow. This resulted in disorientation and the fish falling back to the downstream end. A more suitable chamber size of 1.80 x 0.50 x 0.26 m (length x width x depth) was eventually chosen. This chamber size continued to provide ample space for burst swimming and manoeuvrability while reducing the

occurrence of fish falling back to the downstream end. The use of the floating plexiglass cover (positioned on the water surface) helped to prevent the flatfish from swimming near the surface and protruding their snout out of the water. Plaice were found to perform best under conditions of subdued lighting. All endurance trials were thus conducted at an ambient light level of approximately 3.1 lux.

A standardized routine was developed for testing the endurance of plaice. This began by haphazardly choosing a fish from one of the holding tanks and placing it into the swimming chamber. A minimum period of 10 min was then provided for acclimation before endurance testing. A nominal flow of 0.10 m/s was provided during this period and the fish tended to settle on the chamber floor, often orienting against the direction of water flow. Following the acclimation period, the chamber belt and downstream electrodes were activated and the flow velocity[1] was gradually increased to 0.30 m/s. A pulsing stimulus (2 Hz) with peak voltage of approximately 8 V was applied across the downstream electrodes to encourage the fish to swim against the flow until exhaustion. See Appendix 1 for a summary of the experimental setup.

A Hi-8 video camera was installed for the monitoring and recording of plaice swimming activities. The camera was positioned with a field of view through the large plexiglass side of the flume, similar to that shown in Figure 2.2. Post-analysis of the video footage was conducted to help determine which swimming trials should be

---

[1]At speeds exceeding 0.30 m/s, disorientation and panic-like behaviour was increasingly observed and most fish failed to swim continuously.

excluded from the statistical analysis. Trial results were excluded on the basis of two criteria: a) if the fish was unable to achieve the target swimming speed of 0.30 m/s, or b) if once achieving the target swimming speed, the fish then sat on the chamber bottom at the downstream end and ceased swimming. In trials where the latter was observed, these fish were not considered exhausted, just uncooperative for reasons unknown, and did not fit the established exhaustion criteria (see Section 2.3, Measuring Endurance).

3.3 Results

A total of 228 swimming trials were completed during the 16-week experiment. The majority of these fish failed to reach the target swimming speed of 0.30 m/s for suitable endurance testing and were therefore excluded from the analysis. Several trials were also excluded due to the fish continuously sitting on the chamber floor at the downstream end and refusing to swim. This left a total of 98 successful swimming trials (Table 3.1), in which 88 plaice swam to exhaustion and 10 plaice were censored after failing to exhaust within 200 min. Only the larger fish were found to have endurance greater than 200 min ($\bar{x}$ = 35.8 cm, s.d. = 5.1) and were observed at water temperatures ranging from 0.3 to 9.7 C ($\bar{x}$ = 4.0 C, s.d. = 3.6).

It was found that endurance increased with increasing fish length and water temperature (Fig. 3.1 and 3.2). For plaice between 15 and 20 cm in length, the average endurance was 1.5 min (s.d. = 1.2) at temperatures from 0.0 to 2.0 C, rising slightly to 2.6

min (s.d. = 1.2) at temperatures from 6.0 to 8.0 C. By comparison, larger plaice between 35 and 40 cm in length had an average endurance of 36.5 min (s.d. = 29.9) at temperatures from 0.0 to 2.0 C, rising to 76.3 min (s.d. = 47.1) at temperatures from 6.0 to 8.0 C. Small fish (< 25 cm) typically showed a burst-and-glide swimming strategy and were usually observed struggling to swim away from the downstream end of the flume. Larger fish (> 25 cm) had greater swimming capability and tended to use either a steady cruising or a swim-and-settle strategy. The latter behaviour was characterized by repeatedly swimming to the upstream end of the chamber followed by settling on the floor and riding back on the moving belt. Some variability in endurance is suspected to have occurred due to between-individual differences in swimming strategy. Many of the fish were observed switching to a burst-and-glide swimming strategy when nearing exhaustion.

The results of the failure time analysis (Table 3.2) indicate that both fish length and water temperature had a significant effect[2] ($p < 0.0001$, $p = 0.012$) on the predicted endurance hazard rate. Fish length provided the greatest reduction in the log likelihood statistic followed by water temperature. The partial correlation with the endurance hazard rate (see Norušis, 1994) was reasonable for fish length ($R = -0.258$) but low for water temperature ($R = -0.078$). The interaction term for fish length and water temperature was not statistically significant ($p > 0.05$) to warrant inclusion in the model. The negative

[2]The effect of water temperature found in this study was not detected in the preliminary analysis of the data using multiple regression analysis (Winger et al., 1997).

regression coefficients for fish length and water temperature indicates that given the baseline rate of failure[3], the hazard rate for an individual fish is decreased with increasing fish length and water temperature. This decline in the hazard rate is equivalent to an increase in the endurance probability. In other words, the probability of a fish achieving an endurance greater than time t is increased with increasing fish length and water temperature.

There were no obvious trends in the partial residual plots or DfBeta plots for fish length and water temperature. However, three potentially influential endurance times were noted (Fig. 3.3) including: a) a 26 cm plaice which demonstrated an endurance time of 163 min, and b) both a 30 and 31 cm plaice which exceeded an endurance of 200 min despite the relatively low temperatures of 0.5 and 0.8 C respectively. While these endurance times were high compared to other fish of the same length and temperature, there was no biological or technical reason for eliminating them from the analysis. It was concluded that the endurance times for plaice resulted in a good fit of the Cox proportional hazards model.

Estimates of endurance probability, $S(t)$, were calculated from the predicted endurance hazard rates, $h(t)$, and some examples of probability curves for different fish lengths and water temperatures are illustrated in Figures 3.4a-d. From these figures it is evident that the probability of achieving an endurance greater than time t increases

---

[3]The baseline hazard rates for the observed swimming endurance times for American plaice are presented in Appendix 2.

rapidly with increasing fish length and water temperature. For example, at 0.0 C the probability that plaice has endurance greater than 10 min is near 0% for a 15 cm fish, 18% for a 25 cm fish, 73% for a 35 cm fish, and 94% for a 45 cm fish. By comparison, an increase in water temperature is shown to improve the probability of a 15 cm fish achieving an endurance of two min from 21% at 0.0 C to 52% at 9.0 C.

Dissolved oxygen content within the flume remained high throughout the experiment. The mean concentration was 11.8 mg O_2/L (s.d. = 1.3) with the percent of dissolved oxygen saturation never falling below 83.5%. The mean concentration for the censored endurance trials ($\bar{x}$ = 11.6 mg/L, s.d. = 1.5) was not statistically different (two-tailed t-test, p = 0.604) from the mean concentration for trials where endurance was less than 200 min ($\bar{x}$ = 11.9 mg/L, s.d. = 1.3).

3.4 Discussion

Flatfish Behaviour:

Encouraging flatfish to swim in flumes has achieved only moderate success in previous studies (Beamish, 1966; Priede and Holliday, 1980; Duthie, 1982). Rheotactic behaviour is typically observed in the presence of a water current in which flatfish tend to rest on the bottom and cease swimming (Arnold, 1969). Using a horizontal Blažka-type respirometer, Beamish (1966) reported that winter flounder could not be induced to swim at speeds less than 0.75 m/s. This problem was later addressed by Priede and Holliday

(1980) who developed a tilting Brett-type respirometer to test the critical swimming speeds (U_{crit}) and oxygen consumption of North Sea plaice. Here, the flume was tilted forward at an angle of approximately 60°, forcing the fish to slip off the bottom and swim in a downhill direction. While this design encouraged flatfish to swim at slower speeds, it was found to reduce the power (energy) requirement for swimming and therefore bias estimates of oxygen consumption. Priede and Holliday (1980) also reported that many of their fish never performed satisfactorily, often facing in the wrong direction or becoming disoriented when the swimming speed was increased. Similar difficulties using the same apparatus were also found by Duthie (1982) in his studies of critical swimming speeds (U_{crit}) and oxygen consumption in European flounder, common dab, and lemon sole.

In this study, an alternative flume design was used for encouraging flatfish to swim continuously at slow speeds until exhaustion. The presence of a moving belt as the floor of the swimming chamber was sufficient stimulus to induce American plaice to swim continuously, thus preventing rheotactic behaviour. The energetic bias due to swimming downhill (Priede and Holliday, 1980; Duthie, 1982) and the use of high flow speeds to induce swimming (Beamish, 1966) were eliminated in this flume design.

Swimming Endurance:

The results of the failure time analysis revealed that fish length had a significant effect on the endurance hazard rate. This is sufficient evidence to reject the null hypothesis that endurance is independent of fish length. The endurance demonstrated by this species, especially the larger individuals, far exceeds any previous laboratory observations of flatfish swimming performance. In trials where endurance exceeded 200 min (speed = 0.30 m/s), this is equivalent to travelling a minimum distance of 3.6 km. This is quite surprising given the relatively sedentary and nonmigratory behaviour reported for this species. Tag and recapture data collected on the Grand Bank of Newfoundland found that most plaice were recovered less than 25 nautical miles from the release site up to seven years after tagging (Pitt, 1969). The findings from this study suggest that this species would be capable of rather lengthy migrations given its apparent swimming capability. Studies on the migratory behaviour of North Sea plaice (Harden Jones, 1980; Metcalfe et al., 1990) have shown that this flatfish species, in contrast, is capable of swimming considerable distances with the aid of tidal-stream transport. Observations of acoustically tagged fish (length = 42 cm; temp. = 7.4 C) revealed an average distance travelled of 12.6 km when swimming in the direction of the tide during a single 12.5 h tidal cycle (Metcalfe et al., 1990). However, the authors found that the fish travelled further than the distance predicted from passive transport, indicating that active swimming was also involved. It was calculated that relative to the tide, the average

distance travelled was 4.3 km with a swimming speed of approximately 0.24 m/s. This is remarkably close to the maximum stamina recorded for American plaice (i.e. 3.6 km) at 0.30 m/s in the current study. Despite the dangers of comparing field observations with laboratory data, these findings suggest that the endurance of these two species may be comparable.

The results of the failure time analysis also revealed that water temperature had a significant effect on the endurance hazard rate. This is sufficient evidence to reject the null hypothesis that endurance is independent of water temperature. These findings are consistent with the temperature related effects reported for North Sea plaice, European flounder and winter flounder (Blaxter and Dickson, 1959; Beamish, 1966; Priede and Holliday, 1980; Duthie, 1982). However, based on the relatively low partial correlation between water temperature and the endurance hazard rate ($R = -0.078$), it appears that water temperature has only a weak effect (albeit significant) on the endurance of plaice. This is also demonstrated by the relatively weak trend shown in Figure 3.2. A weak temperature effect was also reported by Beamish (1966) on the endurance of winter flounder. The author found that endurance improved only at the highest temperature treatment of 14.0 C, with no appreciable trend across the lower 5.0, 8.0, and 11.0 C temperature treatments. These studies suggest that water temperature alone is not a major factor affecting the swimming endurance of flatfish species.

General observations showed that plaice are capable of a number of swimming

strategies. Combinations of cruising, burst-and-glide, and swim-and-settle strategies were frequently observed during the experiment. While fish length appeared to be a factor in determining swimming strategy, it was not uncommon to observe fish (> 25 cm) of equal size at similar water temperatures using different strategies. It is therefore suspected that some between-individual variation in endurance may have existed due to differences in swimming strategy. Whether these strategies vary in energetic cost (in terms of endurance) has not been investigated. However, theoretical calculations of the cost of swimming (in mg O_2 consumed per unit distance travelled) have suggested that it would be uneconomical for negatively buoyant flatfish to swim at speeds below 0.6 BL/s (Priede and Holliday, 1980; Duthie, 1982). Both of these studies have also reported that the theoretically most optimal swimming speeds should be closely correlated with the critical swimming speeds (U_{crit}) for flatfish species. The studies concluded that the aerobic scope of certain flatfish species may be insufficient to allow them to swim at what is theoretically their most optimal swimming speeds. As a result, both papers have speculated that, over long distances, flatfish may adopt anaerobic swimming strategies such as bursting followed by periods of rest to counter balance the accrued oxygen debt. The findings from this study have shown that American plaice are capable of employing different swimming strategies and that the ability to employ certain strategies appears to be somewhat dependent on fish length. Whether certain strategies were more effective than others at maximizing endurance was not investigated. Further studies should be

directed toward examining these strategies and quantifying their effect on endurance. Video analysis of flatfish swimming kinematics, in particular, has been largely unexplored and would prove valuable to the understanding of flatfish swimming energetics. Of major interest would be information on the tail-beat frequencies, tail-beat amplitudes and stride length for comparison against roundfish.

Table 3.1. Descriptive statistics for 98 successful swimming endurance trials for American plaice (*Hippoglossoides platessoides*) at different temperatures.

Temperature (C)	No. of Fish	Length range (cm)	Mean Length (s.d.) (cm)
-0.2 to 1.9	38	18 to 44	32.05 (6.14)
2.0 to 3.9	26	14 to 41	28.81 (8.00)
4.0 to 5.9	9	22 to 38	31.00 (4.92)
6.0 to 7.9	17	17 to 40	29.71 (7.97)
8.0 to 9.9	8	29 to 42	33.88 (4.67)

Table 3.2. Failure time analysis of the swimming endurance of American plaice (*Hippoglossoides platessoides*) using the Cox proportional hazards model. Variables were entered into the regression model using forward stepwise selection. The significance of the variables were tested on the basis of their reduction of the log likelihood value for the model. The likelihood-ratio test statistic (χ^2) is defined as -2(log likelihood before variable added - log likelihood after variable added).

Variables in the Model

Step number	Variable	Coefficient (SE)	Log likelihood of model	χ^2	df	p	R
0	---	---	-339.468	---	---	---	---
1	Fish Length (cm)	-0.169 (0.025)	-313.468	52.002	1	<0.0001	-0.258
2	Temperature (C)	-0.095 (0.038)	-310.282	6.371	1	0.0116	-0.078

Global χ^2	df	p
55.977	2	<0.0001

Variables not in the Model

Variable	Score	df	p
Fish Length x Temperature	0.006	1	0.937

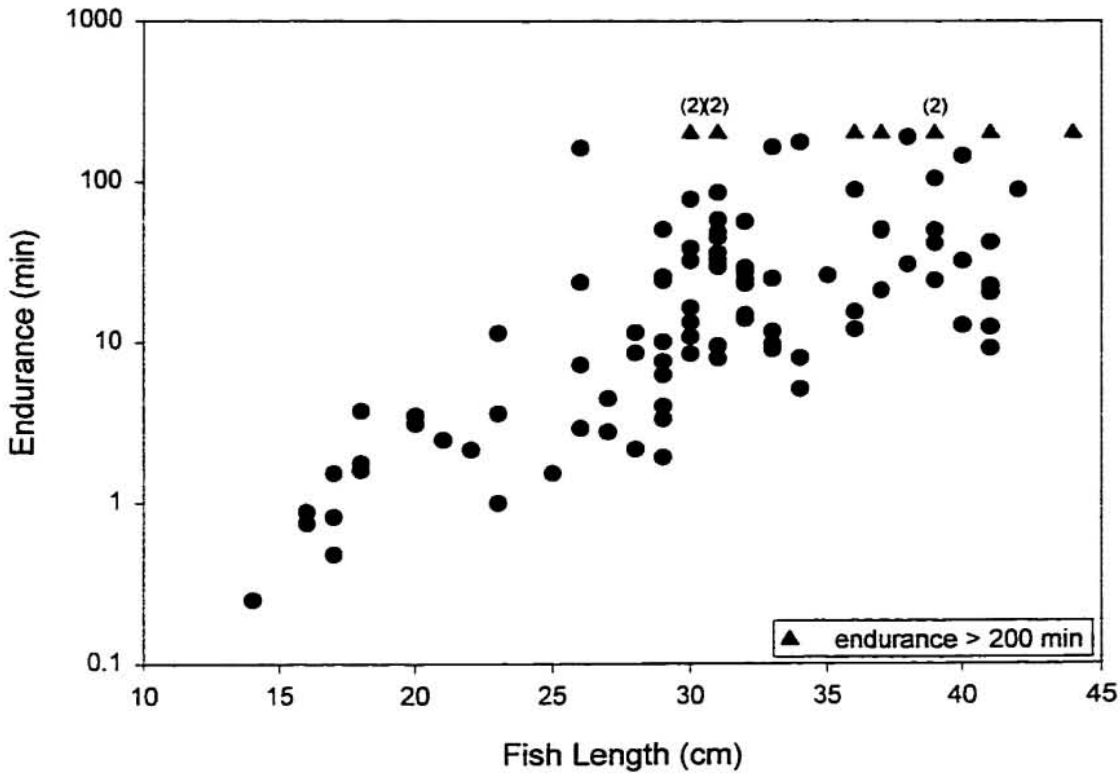

Figure 3.1. Logarithm of endurance (min) of American plaice (*Hippoglossoides platessoides*) plotted against fish length (cm). Values in parentheses represent the number of fish (> 1) still swimming at the end of the 200 min test period.

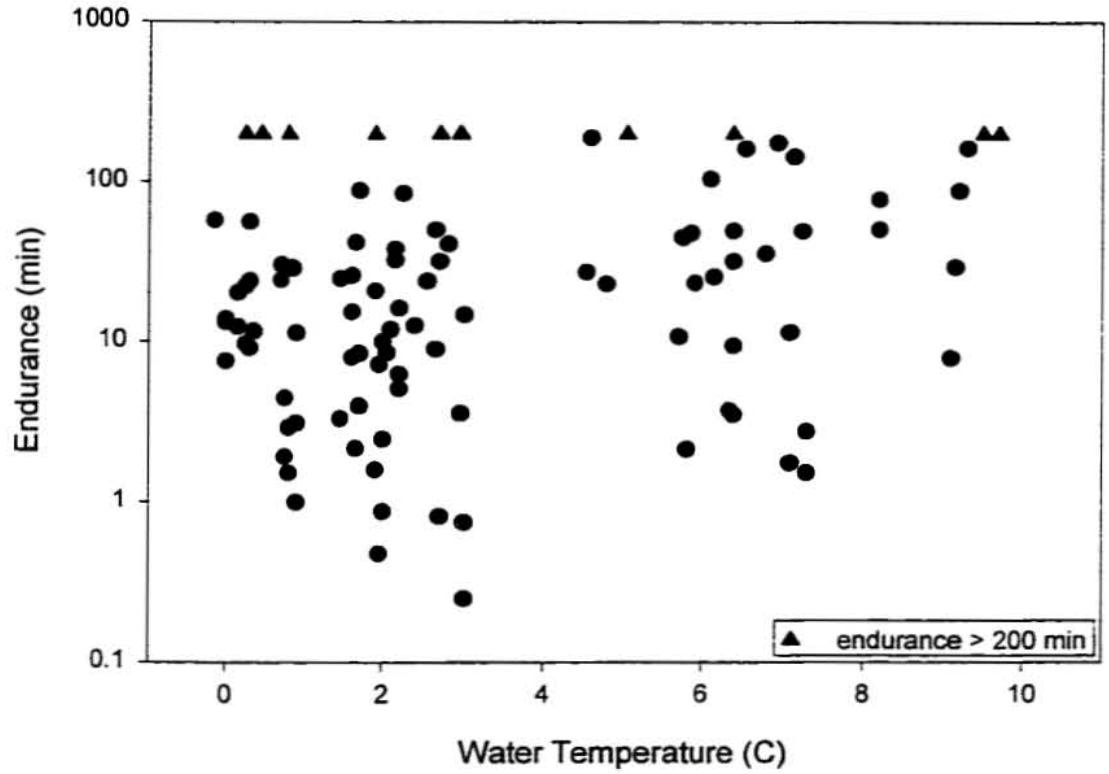

Figure 3.2. Logarithm of endurance (min) of American plaice (*Hippoglossoides platessoides*) plotted against water temperature (C).

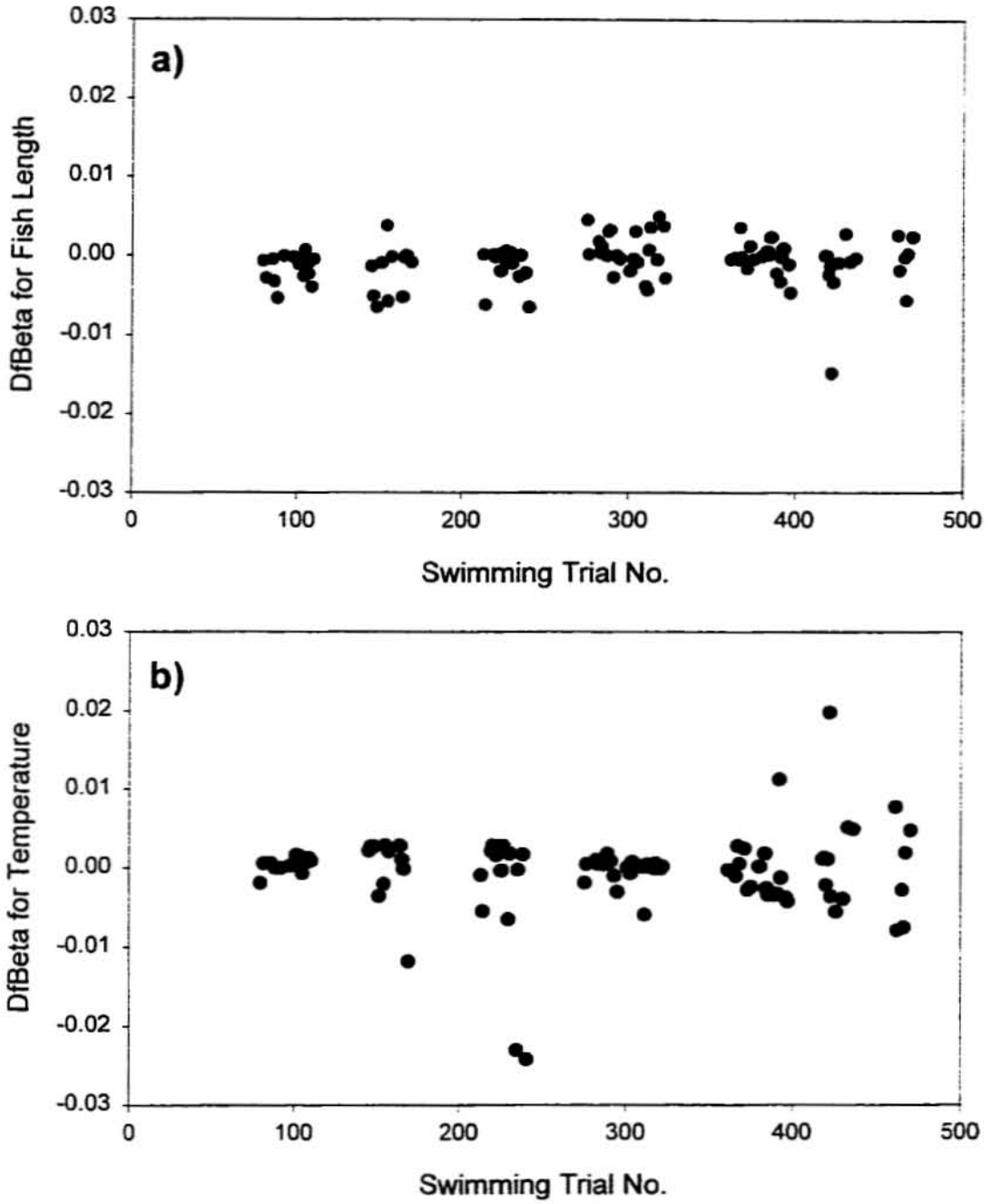

Figure 3.3. DfBeta statistics for a) fish length and b) water temperature plotted against each swimming endurance trial number for American plaice (*Hippoglossoides platessoides*). The DfBeta statistic is an estimate of the change in the regression coefficient with and without the swimming trial included in the analysis.

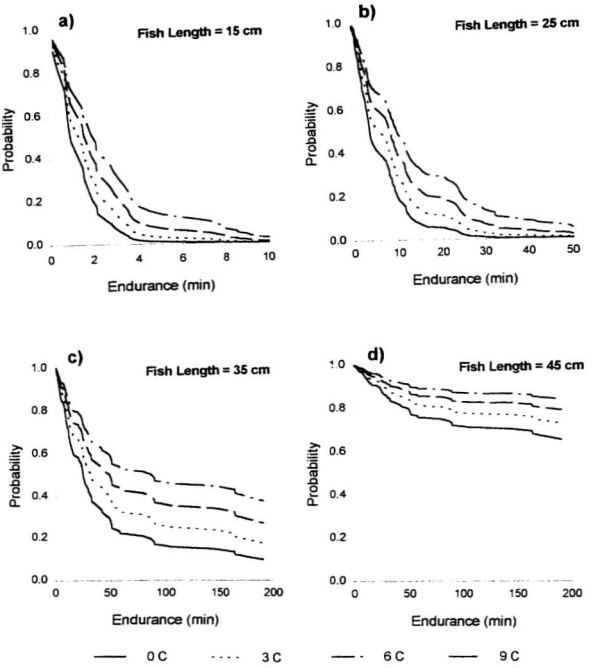

Figure 3.4. Estimated probability curves for the swimming endurance of American plaice (*Hippoglossoides platessoides*) at different water temperatures for fish lengths a) 15 cm, b) 25 cm, c) 35 cm, and d) 45 cm.

Chapter 4. Swimming Endurance of Atlantic Cod

4.1 Introduction

Considerable research has been conducted on various aspects of the swimming performance of Atlantic cod. This has included experiments relating to maximum burst speeds (Blaxter and Dickson, 1959), exercise physiology (Beamish, 1968; Nelson et al., 1994), oxygen consumption (Soofiani and Priede, 1985), kinematics of swimming (Videler and Wardle, 1978), twitch contraction frequencies (Wardle, 1980; Videler and Wardle, 1991), and swimming endurance (Beamish, 1966; He, 1991). Studies on the endurance of cod have directly investigated the effects of swimming speed and water temperature. Beamish (1966) used a small Blažka-type respirometer to test the endurance of cod (35 - 36 cm) native to the relatively warm waters of the Bay of Fundy region. The author tested endurance at swimming speeds ranging from 0.75 to 1.35 m/s and at temperature treatments of 5.0 and 8.0 C. He (1991) used a much larger flume to test the endurance of cod (36 - 52 cm) native to the colder waters off the east coast of Newfoundland and Labrador. Here, swimming speeds ranged from 0.42 to 1.36 m/s and temperatures ranged from -0.3 to 1.4 C. A comparative analysis of the datasets from both studies by He (1991) indicated the likelihood of a significant temperature effect on the endurance of cod at speeds less than or equal to 1.0 m/s. Neither Beamish (1966) nor He (1991) directly investigated the effect of fish length on the endurance of cod.

The purpose of this experiment was to conduct a systematic investigation into the

factors affecting the swimming endurance of cod native to the colder waters off the east coast of Newfoundland and Labrador. Three hypotheses were tested: a) endurance will decrease with increasing swimming speed, b) endurance will increase with increasing fish length, and c) endurance will increase with increasing water temperature. The results are discussed in relation to other cod endurance studies, and in Chapter Five the data are used to illustrate the implications for trawl catchability.

4.2 Materials and Methods

Endurance trials were completed over a duration of 32 weeks from November 1996 to July 1997. This experiment was conducted concurrently with the American plaice experiment discussed in Chapter Three. Measures of endurance were recorded for cod ranging in length from 41 to 86 cm ($\bar{x}$ = 57.8 cm, s.d. = 10.5). Trials were conducted opportunistically at water temperatures ranging from 0.0 to 9.8 C ($\bar{x}$ = 3.2 C, s.d. = 2.8) as the ambient temperature of incoming coastal seawater changed across seasons.

Pilot trials were conducted during October of 1996 to determine which experimental conditions would best encourage cod to swim. In keeping with the methods of He (1991), a chamber size of 1.80 x 0.50 x 0.46 m (length x width x depth) was used. This reduction of the chamber size was necessary in order to test the endurance of cod at speeds greater than 1.00 m/s (see Section 2.2, Apparatus). Similar to He (1991), cod were found to swim comfortably up to a maximum speed of 1.30 m/s. At speeds

exceeding 1.30 m/s, flow turbulence within the chamber increased substantially and cod were observed struggling to swim against the flow. As a result, swimming speed treatments were chosen between 0.80 and 1.30 m/s, at increments of 0.10 m/s. A number of additional trials were also conducted at 0.60 m/s, but only for temperatures less than 3.0 C. The floating plexiglass cover was not used in this experiment since it was not suitable for use at high speeds. Consistent with the methods of He (1991), an area of bright light was projected near the downstream end of the swimming chamber which created a gradient of light along the length of the chamber. This light gradient encouraged cod to swim toward the upstream end of the chamber and away from the downstream electrodes. Light levels were 1.44×10^4 lux, 1.28×10^1 lux, and 6.35 lux for the downstream, midstream, and upstream ends of the swimming chamber respectively. The electrical stimulus emitted from the downstream electrodes was applied at a frequency of 2 Hz with peak voltage of approximately 15 V. See Appendix 1 for a summary of the experimental setup.

A standardized routine was developed for testing the endurance of cod. This began by haphazardly choosing a fish from one of the holding tanks and randomly assigning it a swimming speed for endurance testing. The fish was then placed into the swimming chamber and given a minimum period of 10 min for acclimation. A nominal flow of 0.10 m/s was provided during this time. This was followed by a 10 min *orientational* swim at 0.50 BL/s (V_o). The chamber belt, downstream lighting, and

electrodes were activated at the beginning of the orientational swim. If the *target speed* (V_t) was less than 1.00 BL/s, the swimming speed was gradually increased from V_o to V_t over a period of 5 min. If however V_t was greater than 1.00 BL/s, then the orientational swim was followed by an extra *conditional* swim at 1.00 BL/s (V_c) for an additional 5 min. Following the conditional swim, the swimming speed was gradually increased from V_c to V_t over the next 5 min. This two-tiered routine was adopted from He (1991) and has been found to be an effective means for conditioning cod to swim at speeds greater than 1.00 BL/s.

4.3 Results

A total of 229 swimming trials were completed during the 32-week experiment. Almost one-third of these fish failed to reach their target swimming speed (V_t) for suitable endurance testing and were therefore excluded from the analysis. This left a total of 154 successful swimming trials (Table 4.1), in which 139 cod swam to exhaustion and 15 cod were censored after failing to exhaust within 200 min. Censored trials were observed only at the slower swimming speeds of 0.60 and 0.80 m/s. Seventy-five percent of the fish tested at 0.60 m/s had endurance times exceeding 200 min compared to only 10% of the fish tested at 0.80 m/s. These censored trials consisted of fish ranging in length from 42 to 70 cm ($\bar{x}$ = 56.1 cm, s.d. = 8.5) and at temperatures ranging from 0.1 to 2.7 C ($\bar{x}$ = 1.2 C, s.d. = 1.1).

Swimming speed was the only factor found to affect the endurance of cod. A decreasing trend in the logarithm of endurance with increasing swimming speed was found (Figure 4.1). The mean endurance at 0.60 m/s was 50 min, with the endurance of some individuals falling to less than 1 min at speeds exceeding 1.10 m/s. At lower speeds the dominant swimming strategy was typically cruising, while a combination of cruising and burst-and-glide swimming was always observed at higher speeds. However, it was not uncommon to observe fish of equal size at similar water temperatures using different swimming strategies. It is therefore suspected that some individual variation in endurance may have existed due to differences in swimming strategy. Moreover, many of the fish were observed switching to a burst-and-glide swimming strategy when nearing exhaustion. No significant relationship was found between endurance and the independent variables fish length and water temperature (Figures 4.2 and 4.3).

The results of the failure time analysis (Table 4.2) indicate that swimming speed had a highly significant effect ($p < 0.0001$) on the endurance hazard rate. The partial correlation (see Norušis, 1994) between swimming speed and the endurance hazard rate was 0.361. The remaining variables for fish length, water temperature and the four interaction terms were not statistically significant ($p > 0.05$) and did not warrant inclusion in the model. The positive coefficient for speed indicates that given the baseline rate of failure[4], the hazard rate for an individual fish is increased with increasing swimming

[4]The baseline hazard rates for the observed swimming endurance times for Atlantic cod are presented in Appendix 3.

speed. This increase in the hazard rate is equivalent to a decrease in the endurance probability. In other words, the probability of a fish achieving an endurance greater than time t is decreased with increasing swimming speed.

There was no obvious trend in the partial residual plot or DfBeta plot for swimming speed, however, one potentially influential endurance time was noted (Fig. 4.4). This was a cod which demonstrated an endurance time greater than 16 min at a swimming speed of 1.20 m/s (length = 47 cm, temp. = 6.9 C). While this endurance time is high compared to the other fish tested at the same speed, there was no biological or technical reason for eliminating the trial from the analysis. It was concluded that the swimming endurance times for cod resulted in a good fit of the Cox proportional hazards model.

Estimates of endurance probability, $S(t)$, were calculated from the predicted endurance hazard rates, $h(t)$, and some examples of probability curves for different swimming speeds are illustrated in Figure 4.5. It is shown that the probability of achieving an endurance greater than time t decreases rapidly with increasing swimming speed. For example, the probability that cod has endurance greater than 10 min is 95% at 0.60 m/s, dropping to 27% at 1.00 m/s, and less than 0% at speeds equal to or greater than 1.20 m/s.

Dissolved oxygen content within the flume remained high throughout the experiment. The mean concentration was 13.2 mg O_2/L (s.d. = 1.8) with the percent of

dissolved oxygen saturation never falling below 85.9%. However, the mean concentration for the censored endurance trials ($\bar{x}$ = 14.6 mg/L, s.d. = 1.4) was found to be significantly different (two-tailed t-test, p = 0.001) from the mean concentration for trials where endurance was less than 200 min ($\bar{x}$ = 13.1 mg/L, s.d. = 1.8). This difference is believed to be attributed to the fact that the censored trials were observed only at the lower temperatures (0.1 to 2.7 C) when the ambient oxygen concentrations of the incoming seawater were generally higher. It is not suspected that the elevated levels of oxygen concentration were associated with improved endurance (i.e. endurance greater than 200 min).[5]

4.4 Discussion

The results of the failure time analysis revealed that swimming speed had a significant effect on the endurance hazard rate for cod. This finding provides sufficient evidence to reject the null hypothesis that endurance is independent of swimming speed. This is consistent with the speed effects reported by Beamish (1966) and He (1991). In those studies, the authors found that the logarithm of endurance for cod decreased linearly with increasing swimming speed. A similar relationship was found in this study.

This study marks the first investigation into the effect of fish length on the

---

[5]Preliminary analysis of dataset showed that dissolved oxygen had no significant effect on the endurance hazard rate.

swimming endurance of cod. The results do not support the hypothesis of length-dependent endurance, and as a result, the null hypothesis cannot be rejected. It is not clear why a length effect was not detected. However, one factor which was suspected to have contributed to this finding was the use of a fixed chamber size for all swimming trials, irrespective of differences in fish size. It was recognized that this may have potentially biased the experimental conditions across the range of fish sizes tested. Smaller fish would have enjoyed increased space for manoeuvrability and the opportunity to employ a variety of swimming strategies. By comparison, larger fish swimming in the same chamber may have been disadvantaged compared to smaller fish due to the relative reduction in available space. As a result, larger fish may have been restrained from employing certain swimming strategies. Webb (1993) reported that steelhead trout (*Oncorhynchus mykiss*) swimming in constrained spaces, i.e. small flume chambers, experienced a reduction in the maximum tail-beat amplitude. If this had occurred in the current study, larger cod would have been expected to suffer a reduction in swimming performance through reduced thrust capability. This might have lead to diminished endurance thereby potentially masking any underlying length effect. To test this hypothesis, a post-hoc 'sensitivity analysis' was conducted. The failure time analysis was re-run a number of times following the systematic and successive right-truncation of fish length. Consistent with the initial findings, however, the results did not reveal any significant effect of fish length on the endurance hazard rate. Although not definitive,

these findings indicate that the experimental design was not in fact biased by using a fixed chamber size for the testing of all fish sizes. Further studies should be undertaken to investigate the swimming performance of fish of different lengths in chambers of fixed size. In particular, there is a need for laboratory studies aimed at investigating the swimming capability of very large fish. Most swimming related studies to date have only investigated fish less than 55 cm in length, whereas the current study investigated cod up to and including 86 cm in length.

The effect of water temperature on the endurance of cod may be more subtle than previously thought. The results of this study do not support the hypothesis of temperature-dependent endurance, and as a result, the null hypothesis cannot be rejected. This finding is inconsistent with the temperature effect reported by Beamish (1966). His results showed that cod (35 - 36 cm) at 8.0 C could swim for about 16 min at 1.05 m/s, dropping to only 6 min at 5.0 C at the same speed. In comparison, He (1991) showed that cod of similar size (36 - 42 cm) at approximately 0.0 C could only swim for about 2 min at 1.00 m/s. A comparative analysis of these two datasets by He (1991) indicated the likelihood of a significant temperature effect on the endurance of cod at speeds less than or equal to 1.00 m/s. However, the findings from the current study found no evidence to support the hypothesis of temperature-dependent endurance in cod across the range of temperatures, fish lengths and swimming speeds examined. The endurance times recorded here appear to fall intermittent to those published by He (1991) and Beamish

(1966). This study revealed a mean endurance of roughly 8 min at 0.0 C, 6 min at 5.0 C. and 6 min at 8.0 C for trials similarly at 1.00 m/s.

Cold acclimation may account in part for the undetected effect of temperature on the endurance of cod in this study. It is suspected that thermal compensation at the lower temperatures may have reduced the apparent effect of temperature on endurance. In Newfoundland waters, cod are known to occupy bottom temperatures ranging from -1.5 to 5.5 C depending on the region and season (Lear, 1984; Hutchings and Myers, 1994; Wroblewski et al., 1994; Colbourne et al., 1997). The extension of this species' temperature tolerance into sub-zero conditions may involve some aspect of density-dependent temperature selection, as suggested by Swain and Kramer (1995) for cod in the Gulf of St. Lawrence. Adaptive strategies for survival at low temperatures (e.g. antifreeze substances) are known to exist in cod (Goddard and Fletcher, 1994). It is suggested therefore that other forms of thermal compensation may also exist. Guderley and Blier (1988) argue that in certain species this leads to physiological compensatory responses leading to an increase in the capacity for sustained swimming at low temperatures. These authors outline several types of positive thermal compensation, including changes in muscle contractile properties, myosin ATPase activity, the proportion of red muscle fibers, and the levels of aerobic enzymes in the musculature. Under laboratory conditions, Foster et al. (1993a) found that cold acclimation of cod resulted in higher cytochrome c oxidase (CCO) activity in the white muscle tissues

compared to cod with warm acclimated tissues. Increased CCO activity has been shown to be associated with increased aerobic metabolic rates of tissues (Foster et al., 1993b), supporting the hypothesis of increased aerobic swimming capacity of cod at low temperatures (H. Guderley, Université Laval, Quebec). Whether such thermal responses do in fact improve the swimming capability of cod at low temperatures has not yet been established. However, given that the fish used in this study were maintained under conditions of ambient seawater temperature and ambient photoperiod, it is reasonable to assume that the fish received the natural cues associated with seasonal change. If this is true, then it is speculated that these cod may have had sufficient time to acclimate to the seasonal changes in water temperature, and if capable, the potential to develop thermal compensatory responses prior to endurance testing.

Table 4.1. Descriptive statistics for 154 successful swimming endurance trials for Atlantic cod (*Gadus morhua*) at different temperatures.

Temperature (C)	No. of Fish	Length range (cm)	Mean Length (s.d.) (cm)
0.0 to 1.9	63	43 to 85	59.73 (10.00)
2.0 to 3.9	32	42 to 84	57.38 (10.53)
4.0 to 5.9	27	41 to 86	59.33 (11.99)
6.0 to 7.9	22	41 to 77	52.23 (8.01)
8.0 to 9.9	10	42 to 76	54.30 (10.69)

Table 4.2. Failure time analysis of the swimming endurance of Atlantic cod (*Gadus morhua*) using the Cox proportional hazards model. Variables were entered into the regression model using forward stepwise selection. The significance of the variables was tested on the basis of their reduction of the log likelihood value for the model. The likelihood-ratio test statistic (χ^2) is defined as -2(log likelihood before variable added - log likelihood after variable added).

Variables in the Model

Step number	Variable	Coefficient (SE)	Log likelihood of model	χ^2	df	p	R
0	---	---	-597.332	---	---	---	---
1	Speed (cm/s)	0.082 (0.007)	-504.605	185.455	1	<0.0001	0.361

Global χ^2	df	p
170.390	1	<0.0001

Variables not in the Model

Variable	Score	df	p
Fish length (cm)	1.024	1	0.312
Temperature (C)	2.343	1	0.126
Speed x Fish Length	2.316	1	0.128
Speed x Temperature	3.552	1	0.060
Temperature x Fish Length	2.030	1	0.154
Speed x Temperature x Fish Length	2.723	1	0.099

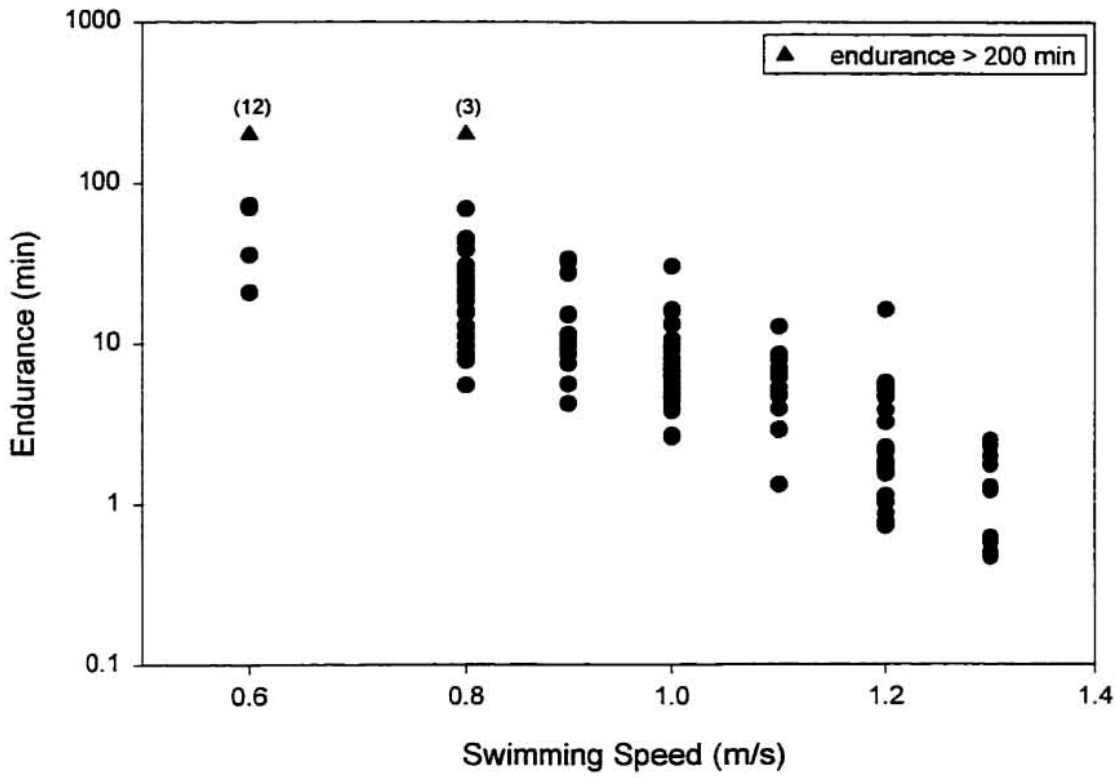

Figure 4.1. Logarithm of endurance (min) of Atlantic cod (*Gadus morhua*) plotted against swimming speed (m/s). Values in parentheses represent the number of fish (> 1) still swimming at the end of the 200 min test period.

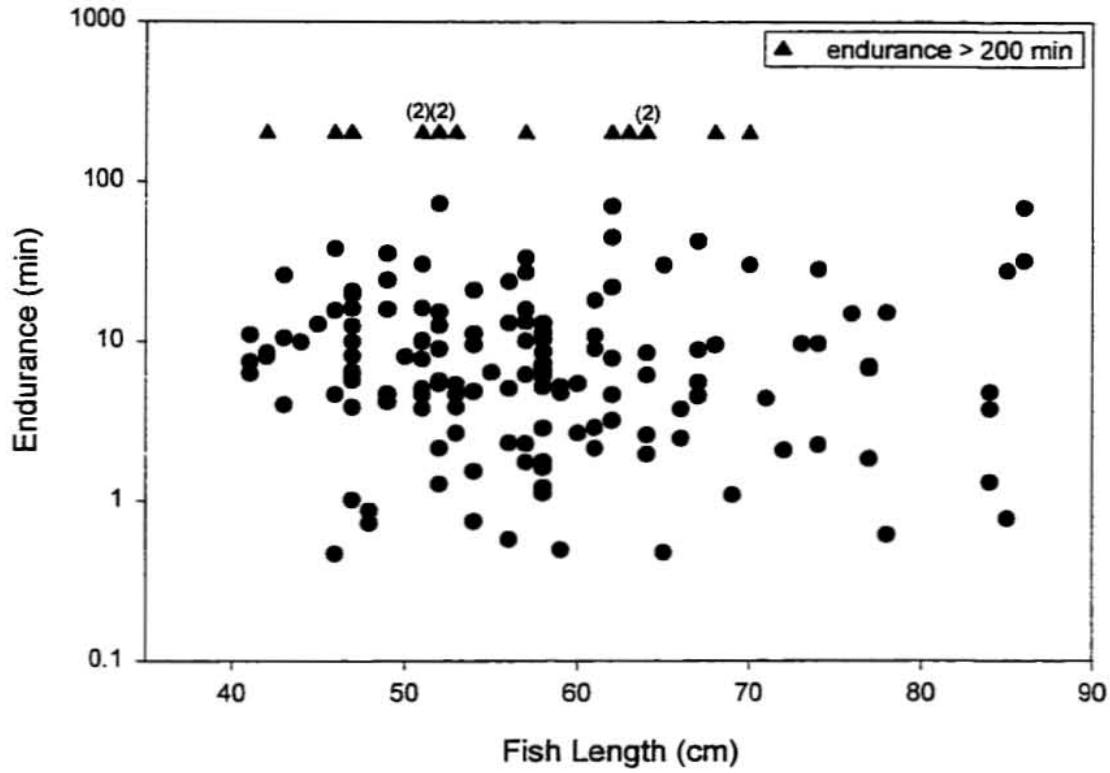

Figure 4.2. Logarithm of endurance (min) of Atlantic cod (*Gadus morhua*) plotted against fish length (cm). Values in parentheses represent the number of fish (> 1) still swimming at the end of the 200 min test period.

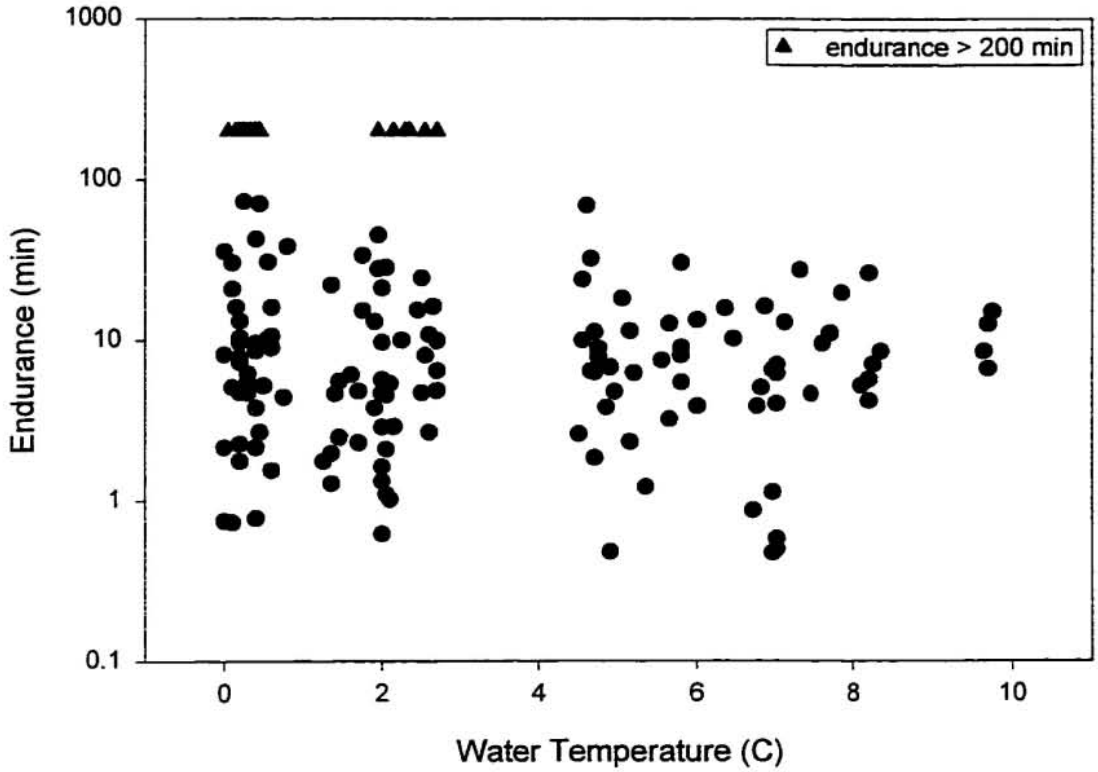

Figure 4.3. Logarithm of endurance (min) of Atlantic cod (*Gadus morhua*) plotted against water temperature (C).

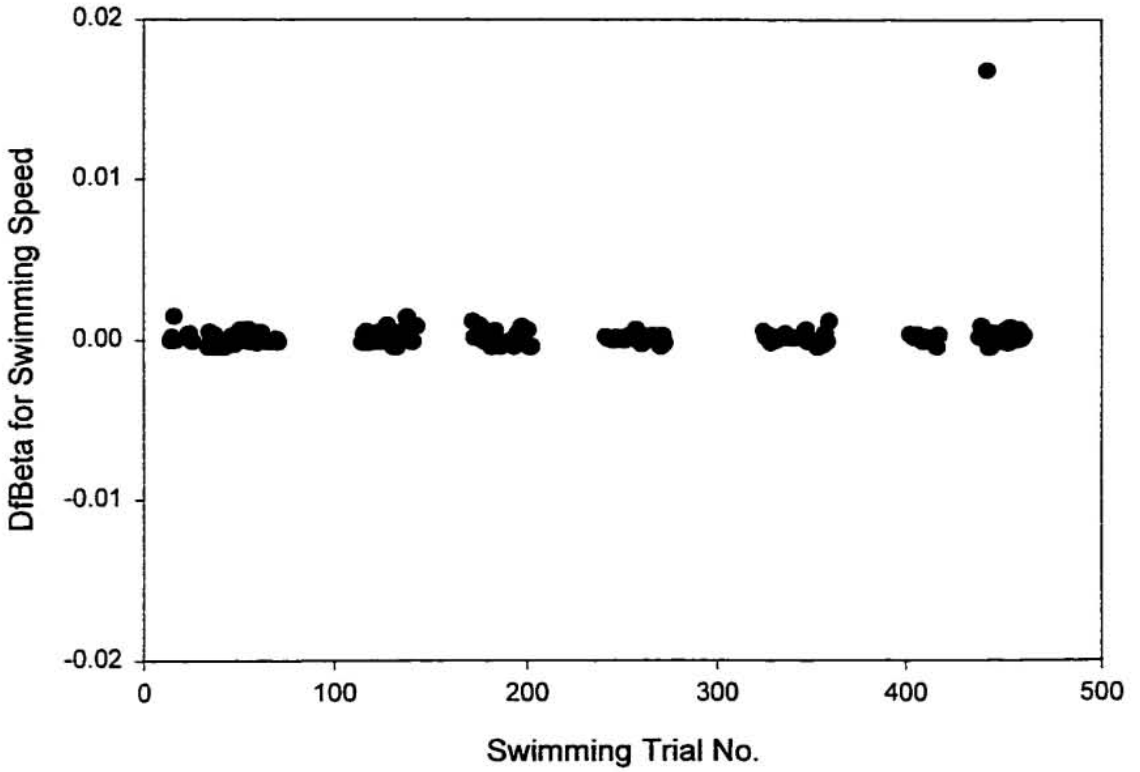

Figure 4.4. DfBeta statistics for swimming speed plotted against each swimming endurance trial number for Atlantic cod (*Gadus morhua*). The DfBeta statistic is an estimate of the change in the regression coefficient with and without the swimming trial included in the analysis.

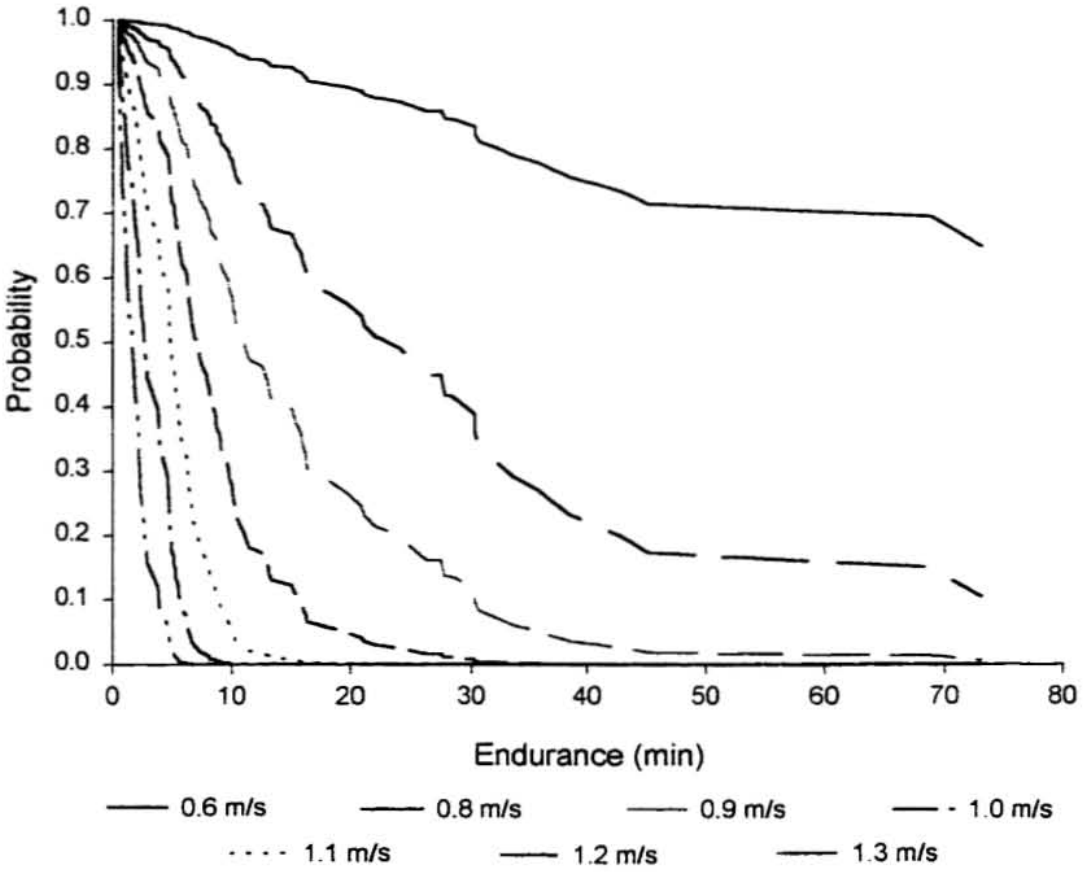

Figure 4.5. Estimated probability curves for the swimming endurance of Atlantic cod (*Gadus morhua*) at different swimming speeds.

Chapter 5. Implications for Trawl Catchability

5.1 American plaice

The estimation and modelling of the herding efficiency of otter trawl sweeps has been the subject of much research in recent years (Harden Jones et al., 1977; Engås and Godø, 1989a; Andrew et al., 1991; Dickson, 1993a, 1993b; Ramm and Xiao, 1995). Unfortunately, little empirical data exist on the herding efficiency of flatfish species. Direct video observations have shown that flatfish are typically herded into the trawl path after contact with the doors, sweeps and sand clouds of the trawl (Main and Sangster, 1981). This behaviour has been described as an incremental process in which the flatfish (once disturbed from the seafloor) swim toward the trawl path in a direction 90° away from the approaching sweeps. After swimming a distance of approximately 0.5 to 5.0 m, the fish settle onto the seafloor once again. Each time the sweeps approach, the flatfish repeat the behaviour and, progressively slip along the sweeps toward the mouth of the trawl (see Figure 5.1). Analogous swimming behaviour was evident during the current laboratory study. Plaice were often observed swimming toward the upstream end of the flume followed by settling on the floor belt and riding back to the downstream end and then repeating the cycle. However, not all of the plaice tested in this study chose the swim-and-settle strategy, many instead opted for steady cruising or burst-and-glide strategies. It is suspected that these different swimming strategies may be employed by flatfish during sweep herding, although direct observations have not been reported.

For flatfish to be effectively herded, the fish must swim at a speed equal or greater than the herding speed of the advancing sweeps and have sufficient endurance to reach the path of the trawl. The distance required to swim is dependent on a) sweep angle, b) the position along the sweep where the fish initially encounter the gear, and c) the angle of avoidance in which the fish choose to swim (Foster et al., 1981). Assuming that plaice swim on average 90° away from an approaching sweep, the swimming requirements to avoid the stimulus and be herded into the trawl path can be roughly estimated. First, the swimming speed of the fish must be at least equal to or greater than the herding speed of the sweeps in order to avoid being overtaken by the gear. The herding speed of sweeps (U_H) is defined as:

$$U_H = \sin\theta \cdot U_T$$

where θ is the sweep angle, i.e. angle of attack of the sweep to the direction of tow, and U_T is the forward towing speed of the trawl through the water. Second, the fish must also have sufficient endurance to reach the trawl path. The distance required to swim to the trawl path (D_H) is defined as:

$$D_H = \tan\theta \cdot D_W$$

where θ is the sweep angle and D_W is the distance from the wingtip where the fish initially encounters the sweep. For example, Canadian research surveys conducted off the east coast of Newfoundland and Labrador use a Campelen 1800 shrimp trawl rigged with 40 m sweeps (McCallum and Walsh, 1995). Towing speed is standardized at 1.50

m/s and sweep angles are known vary from 7.4 to 22.6° ($\bar{x}$ = 19.2°, CV = 15%) over survey depths of 45 to 750 m (Walsh and McCallum, 1997). This is equivalent to a range in U_H from 0.19 to 0.58 m/s. Depending on the distance from the wingtips where flatfish initially encounter the sweeps of this trawl, D_H will vary from zero up to a maximum of 13.9 m (using θ = 19.2°).

Since the sweep length and sweep angle cannot be optimal for the herding of all fish lengths across all bottom temperatures, it follows that the herding of plaice could be highly size-selective. If the results from the current study are representative of field conditions, then the herding efficiency of plaice (at 0.30 m/s) may be both size- and temperature-dependent. At low temperatures small fish are expected to have a lower probability of sufficient endurance to reach the trawl path. If this happens, the fish will suffer a greater likelihood of being overtaken by the sweeps and effectively escape from the gear. As fish length increases, so should the probability of successfully swimming the required distance. Figure 5.2 shows the estimated probability curves for the distances that plaice of different fish lengths are capable of swimming (at 0.30 m/s) at 0.0 and 6.0 C. The probability of exceeding a given swimming distance is shown to improve with increasing fish length and water temperature. Overlaid within the figure is an illustrative example of an otter trawl with a sweep angle of 11.5° and a forward towing speed (U_T) of 1.50 m/s (i.e. U_H = 0.30 m/s). The vertical dashed lines indicate the distances that plaice would be required to swim in order to reach the trawl path after

initially encountering the sweeps at distances of 40, 60, 80, 100, and 120 m from the wingtip. The corresponding probabilities of successfully reaching the trawl path can be read from the y-axis. For example, at 0.0 C it is shown that 15 cm plaice will have roughly an 80% probability of reaching the trawl path if they initially encounter the sweep 40 m from the wingtip, compared to 40% probability at 120 m from the wingtip. At 6.0 C, these same fish will have nearly a 90% probability at 40 m and 60% probability at 120 m, respectively. Systematic size- and temperature-dependent vulnerability of this nature will largely affect the efficiency of the herding process during otter trawling. Any combination of long sweeps and large sweep angles should result in a reduction in the proportion of plaice effectively herded into the trawl path, especially smaller plaice at low bottom temperatures which encounter the sweeps far from the wingtips. However, given that endurance was tested only at 0.30 m/s in the current experiment, it is recognized that the herding efficiency of trawl sweeps can only be inferred under conditions where U_H approximates 0.30 m/s. Further laboratory studies should be directed toward examining the endurance of plaice across a range of swimming speeds comparable to the herding speeds of trawl sweeps, particularly 0.20 to 0.60 m/s. This would provide the capability to estimate the herding efficiency of trawl sweeps across a wider range of gear performance as well as otter trawl designs.

5.2 Atlantic cod

Direct video observations of fish behaviour in the mouth of an otter trawl have now been collected for a number of groundfish species (Main and Sangster, 1981; Glass and Wardle, 1989; Walsh and Hickey, 1993; Bublitz, 1996; Weinberg and Munro, 1997). These studies have consistently reported that many species, once herded into the trawl mouth, tend to orient in the direction of tow and keep station with the advancing trawl. At this stage in the capture process all species and sizes of fish are stimulated to swim at precisely the speed of the advancing trawl. Differences in swimming endurance determine the degree of vulnerability to capture. Factors which directly affect endurance while swimming in the trawl mouth include the speed of the trawl through the water and fish size (Wardle, 1993; Main and Sangster, 1981). Other factors which are thought to affect endurance but for which direct empirical evidence is still lacking include bottom temperature (e.g. Foster et al., 1981; He, 1993; Smith and Page, 1996), bottom type (Engås, 1994) and fish density (Aglen et al., 1997).

It is well established that the towing speed of a trawl is one of the most critical factors affecting the endurance of fish swimming in the trawl mouth. If the results from the current study are representative of field conditions, then the endurance of cod in the trawl mouth is expected to be highly speed-dependent. The findings indicate that even small changes in the speed of a trawl through the water could dramatically affect the rate of exhaustion, i.e. turn-over rate, of cod swimming in the trawl mouth. Figure 5.3 shows

the estimated probability curves for the endurance of cod at swimming speeds comparable to the towing speeds of otter trawls. Using the Cox proportional hazards model developed in Chapter Four, extrapolated curves for 1.40 and 1.50 m/s are also shown. The median endurance (i.e. where $S(t) = 0.5$) is shown to decline rapidly with increasing swimming speed. At a speed of 1.00 m/s, cod had a median endurance of 7.0 min, dropping substantially to 1.6 min at 1.30 m/s. At higher speeds an even further reduction would be expected. The extrapolated probability curves for the higher speeds reveal a median endurance of 47 s at 1.40 m/s and only 35 s at 1.50 m/s. These endurance times are of similar magnitude to the endurance times reported by Main and Sangster (1981). These authors witnessed from direct video observation that cod (27 - 45 cm) were capable of swimming in the trawl mouth at a towing speed of 1.50 m/s for 20 to 70 s depending on the fish size. The close similarity between the current laboratory model and these empirical observations suggest that the endurance of cod measured under laboratory conditions closely approximates the endurance of cod swimming in the trawl mouth.

The results of the current study suggest that fish length (44 - 86 cm) may not have an appreciable effect on the endurance of cod when swimming in the mouth of a trawl. This finding is inconsistent with the length-dependent endurance directly observed by Main and Sangster (1981) for cod slightly smaller in length (27 - 45 cm). The authors reported that the larger cod were capable of swimming in the trawl mouth for a duration

of approximately 50 - 70 s while smaller individuals tended to exhaust within 20 - 40 s. The undetected effect of fish length in the current study is believed to be attributed (in part) to between-individual differences in swimming strategy. If this is true, then this suggests that the endurance of cod in the trawl mouth may also vary with the choice of swimming strategy. Hydromechanical modelling of different swimming strategies has indicated that burst-and-glide swimming may be up to 4-6 times more energetically efficient than steady cruising alone (for review see Blake, 1983). However, observations of fish swimming in the trawl mouth have revealed instead that a combination of steady cruising interspersed with periods of burst-and-glide swimming are most common (Main and Sangster, 1981; Wardle, 1993). Furthermore, the choice of swimming strategy has been observed to change with the onset of fatigue. Main and Sangster (1981) reported that cod (27 - 45 cm) showed an increase in the frequency of burst-and-glide behaviour when nearing exhaustion. This finding is consistent with the current laboratory study. Many cod were observed switching from steady cruising to a burst-and-glide swimming strategy with the onset of fatigue. This change in behaviour would appear to have adaptive significance during trawling given that it would prolong an individual's endurance thereby increasing its probability of escaping capture.

Bottom topography and fish density have also been suggested as potential factors affecting the swimming strategy and behaviour of fish while swimming in the mouth of a trawl. Perturbations in the performance of the footgear due to rocky bottom have been

shown to disrupt swimming formations of cod and other species (A. Engås, Institute of Marine Research, Bergen, Norway). It has been suggested that cod under these circumstances may suffer reduced endurance due to losses of energy associated with the continual change in swimming direction and speed (Engås, 1994). Qualitative observations from video footage have shown that fish density in the trawl mouth may also affect the swimming strategy and endurance of cod (Aglen et al., 1997). These authors reported that when densities were low (1 or 2 fish) cod exhibited a burst-and-glide swimming strategy and were actively searching for escapement opportunities near the footgear. In contrast, when densities were higher (5 or more fish) cod tended to exhibit a steady cruising strategy and formed a school further ahead of the footgear. Qualitative assessment of the video footage showed that the endurance of cod in the trawl mouth was greater when densities were higher.

Although empirical data has never been presented, it is generally assumed that the catchability of groundfish species is greatly enhanced at low temperatures due to a reduction in swimming capability (e.g. Foster et al., 1981; He, 1993; Engås, 1994; Smith and Page, 1996). Laboratory studies investigating the endurance of cod at different temperatures have supported this hypothesis (Beamish, 1966; He, 1991). However, direct video observations have confirmed that large cod are indeed capable of swimming in the trawl mouth for considerable time and distance at temperatures well below 0.0 C (S.J. Walsh and W. Hickey, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland).

The results of the current laboratory study have suggested that water temperature (0.0 - 9.8 C) may not have an appreciable effect on the endurance of cod when swimming in the mouth of a trawl. It is suspected that the undetected effect of temperature in this study may be attributed to seasonal thermal compensation in swimming endurance as suggested in Chapter Four. If such physiological compensatory responses exist under natural conditions, then the effect of bottom temperature on trawl catchability may be less complicated than previously thought. Future resources will need to be directed toward assessing the complex interaction between temperature, swimming physiology and endurance in order to better estimate the implications of bottom temperature on trawl catchability.

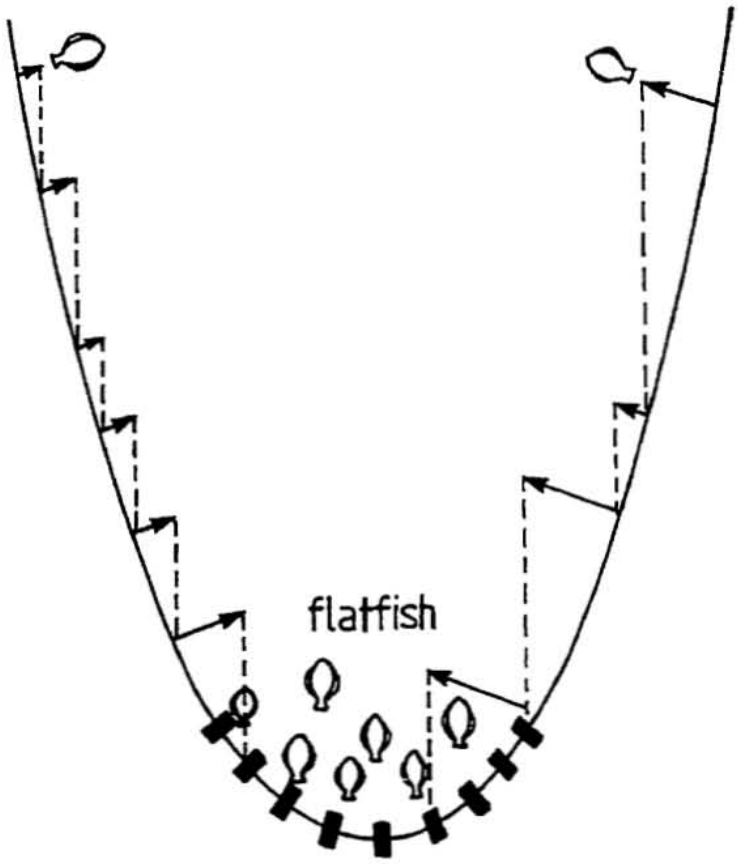

Figure 5.1. Herding behaviour of flatfish toward the mouth of an otter trawl in response to direct contact with the sweeps. The fish are shown to repeatedly swim and settle in a direction 90° to the approaching sweeps (Adopted from Main and Sangster, 1981).

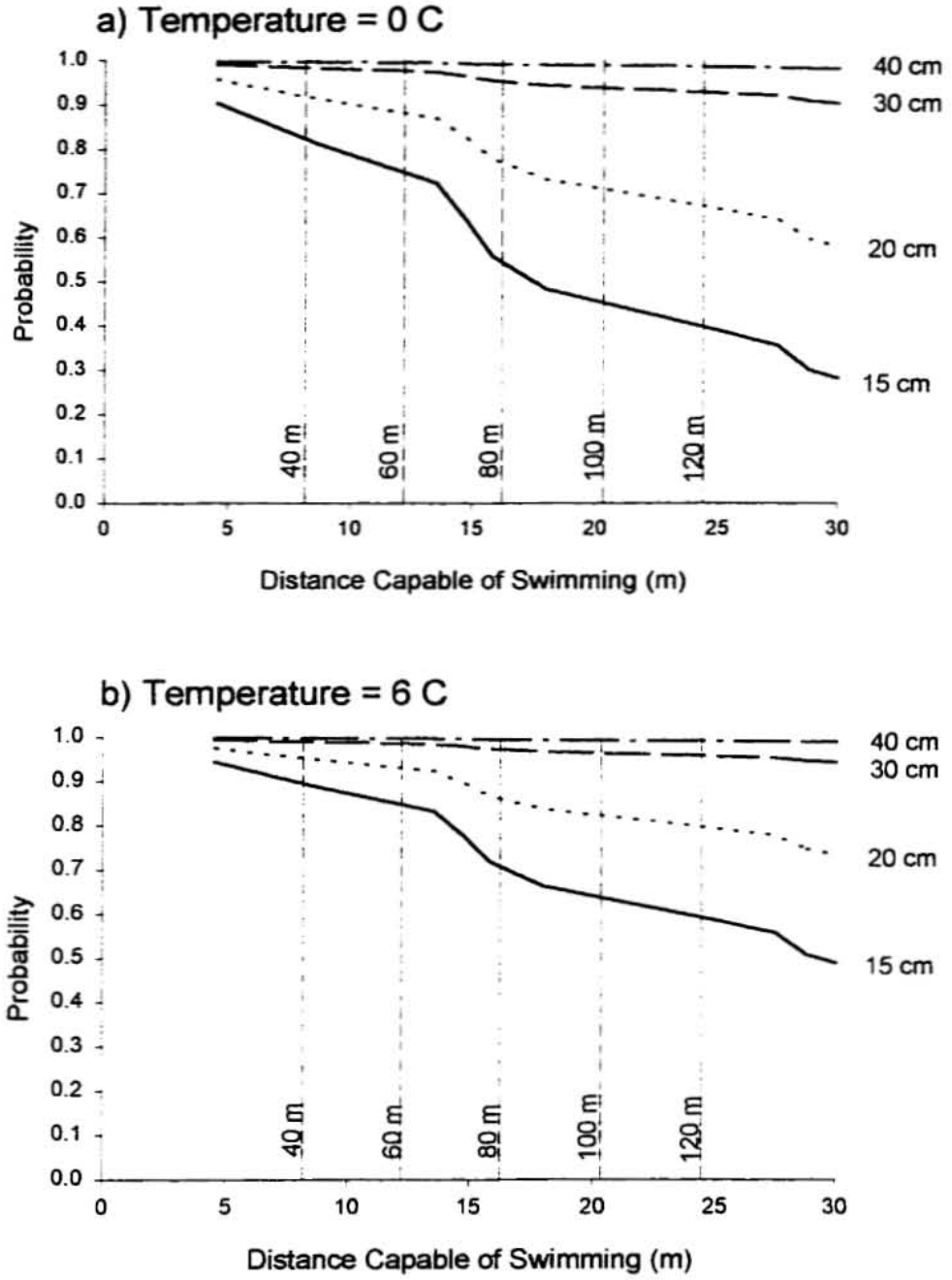

Figure 5.2. Estimated probability curves for the distances capable of swimming (at 0.30 m/s) by American plaice (*Hippoglossoides platessoides*) of different fish lengths at a) 0 C and b) 6 C. Overlaid within the figures is an illustrative example for an otter trawl with a sweep angle of 11.5° and a forward towing speed of 1.50 m/s (i.e. U_H = 0.30 m/s). The vertical dashed lines indicate the distances required to swim in order to reach the trawl path for fish initially encountering the sweeps at 40, 60, 80, 100, and 120 m from the wingtip. Corresponding probabilities of successfully reaching the trawl path can be read from the y-axis.

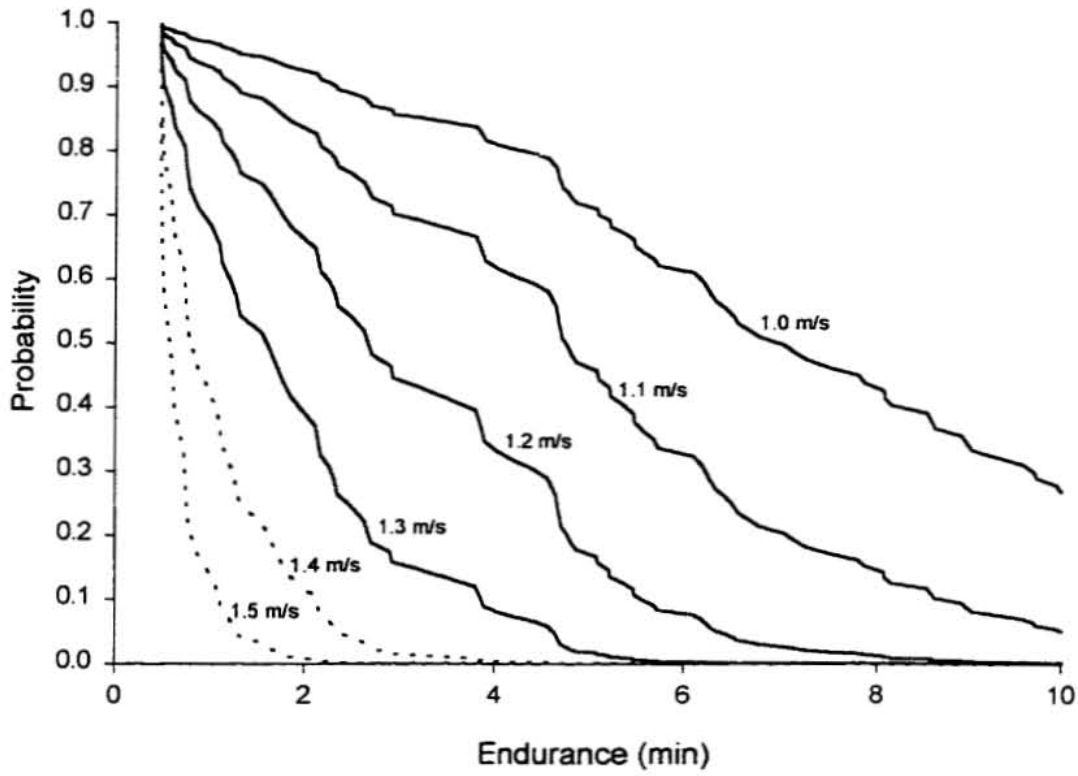

Figure 5.3. Estimated probability curves for the swimming endurance of Atlantic cod (*Gadus morhua*) at swimming speeds comparable to the towing speeds of otter trawls. Solid lines represent swimming speeds tested in the current study. Dashed lines represent extrapolated probability curves using the Cox proportional hazards model developed in Chapter 4.

Literature Cited:

Aglen, A., Engås, A., Godø, O.R., McCallum, B., Stansbury, D., and Walsh, S.J. 1997. Density dependent catchability in bottom trawl surveys. ICES C.M. Doc., No. W:16, 8pp.

Andrew, N.L., Graham, K.J., Kennelly, S.J., and Broadhurst, M.K. 1991. The effects of trawl configuration on the size and composition of catches using benthic prawn trawls off the coast of New South Wales, Australia. ICES J. Mar. Sci., 48:201-209.

Arnold, G.P. 1969. The reactions of plaice (*Pleuronectes platessa*) to water currents. J. Exp. Biol., 51:681-697.

Bainbridge, R. 1960. Swimming and stamina in three fish. J. Exp. Biol., 37:129-153.

Beamish, F.W.H. 1966. Swimming endurance of some Northwest Atlantic fishes. J. Fish. Res. Bd. Can., 23:341-347.

Beamish, F.W.H. 1968. Glycogen and lactic acid concentrations in Atlantic cod (*Gadus morhua*) in relation to exercise. J. Fish. Res. Bd. Can., 25:837-851.

Beamish, F.W.H. 1978. Swimming capacity. In: Fish Physiology, Vol. 7, pp. 101-107. Ed. by W.S. Hoar and D.J. Randall. Academic Press, New York.

Beamish, F.W.H. 1984. Swimming performance of three southwest Pacific fishes. Mar. Biol., 79:311-313.

Bell, W.H., and Terhune, L.D.B. 1970. Water tunnel design for fisheries research. Fish. Res. Bd. Can. Tech. Rep., 195: 69pp.

Blake, R.W. 1983. Fish Locomotion. Cambridge University Press, Cambridge. 208pp.

Blaxter, J.H.S., and Dickson, W. 1959. Observations of the swimming speeds of fish. J. Cons. Int. Explor. Mer, 24:472-479.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Can., 21:1183-1226.

Brett, J.R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. J. Fish. Res. Bd. Can., 24:1731-1741.

Bublitz, C.G. 1996. Quantitative evaluation of flatfish behaviour during the capture by trawl gear. Fish. Res., 25:293-304.

Byrne, C.J., Azarovitz, T.R., and Sissenwine, M.P. 1981. Factors affecting variability of research vessel trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci., 58:258-273.

Colbourne, E., deYoung, B., and Rose, G.A. 1997. Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci., 54(Suppl. 1):149-157.

Cox, D.R., and Oakes, D. 1984. Analysis of Survival Data. Chapman and Hall, London. 201pp.

Cox, D.R. 1972. Regression models and life tables. J. Roy. Stat. Soc. (London) Ser. B. 26:103-110.

Dickson, W. 1993a. Estimation of the capture efficiency of trawl gear. I. Development of a theoretical model. Fish. Res., 16:239-253.

Dickson, W. 1993b. Estimation of the capture efficiency of trawl gear. II. Testing a theoretical model. Fish. Res., 16:255-272.

Duthie, G.G. 1982. The respiratory metabolism of temperature-adapted flatfish at rest and during swimming activity and the use of anaerobic metabolism at moderate swimming speeds. J. Exp. Biol., 97:359-373.

Engås, A. 1994. The effects of trawl performance and fish behaviour on the catching efficiency of demersal sampling trawls. In: Marine Fish Behaviour in Capture and Abundance Estimation, pp. 45-68. Ed. by A. Fernö and S. Olsen. Fishing News Books, Oxford.

Engås, A., and Godø, O.R. 1989a. The effect of different sweep lengths on the length composition of bottom-sampling trawl catches. J. Cons. Int. Explor. Mer, 45:263-268.

Engås, A., and Godø, O.R. 1989b. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer, 45:269-276.

Foster, A.R., Hall, S.J., and Houlihan, D.F. 1993a. The effects of temperature acclimation on organ/tissue mass and cytochrome c oxidase activity in juvenile cod (*Gadus morhua*). J. Fish Biol., 42:947-957.

Foster, A.R., Houlihan, D.F., and Hall, S.J. 1993b. Effects of nutritional regime on correlates of growth rate in juvenile Atlantic cod (*Gadus morhua*): comparison of morphological and biochemical measurements. Can. J. Fish. Aquat. Sci., 50:502-512.

Foster, J.J., Campbell, C.M., and Sabin, G.C.W. 1981. The fish catching process relevant to trawls. Can. Spec. Publ. Fish. Aquat. Sci., 58:229-246.

Glass, C.W., and Wardle, C.S. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fish. Res. 7:249-266.

Goddard, S.V., and Fletcher, G.L. 1994. Antifreeze proteins: their role in cod survival and distribution from egg to adult. ICES Mar. Sci. Symp., 198:676-683.

Godø, O.R. 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. In: Marine Fish Behaviour in Capture and Abundance Estimation. pp. 169-199. Ed. by A. Fernö and S. Olsen. Fishing News Books. Oxford.

Godø. O.R., and Walsh S.J. 1992. Escapement of fish during bottom trawl sampling - implications for resource assessment. Fish. Res., 13:281-292.

Guderley, H. and Blier, P. 1988. Thermal acclimation in fish: conservative and labile properties of swimming muscle. Can. J. Zool., 66:1105-1115.

Gunderson, D.R. 1993. Surveys of Fisheries Resources. John Wiley and Sons, Inc., New York. 248pp.

Harden Jones, F.R., Margetts, A.R., Greer Walker, M., and Arnold, G.P. 1977. The efficiency of the Granton otter trawl determined by sector-scanning sonar and acoustic transponding tags. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 170:45-51.

Harden Jones, F.R. 1980. The migration of plaice (*Pleuronectes platessa*) in relation to the environment. In: Fish Behaviour and Its Use in the Capture and Culture of Fishes, pp. 383-399. Ed. by J.E. Bardach, J.J. Magnuson, R.C. May, and J.M. Reinhart. ICLARM, Manila.

He, P., and Wardle, C.S. 1986. Tilting behaviour of the Atlantic mackerel, *Scomber scombrus*, at low swimming speeds. J. Fish Biol., 29:223-232.

He, P., and Wardle, C.S. 1988. Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L., and saithe, *Pollachius virens* L.. J. Fish Biol., 35:255-266.

He, P. 1991. Swimming endurance of Atlantic cod, *Gadus morhua* L., at low temperatures. Fish. Res., 12:65-73.

He, P. 1993. Swimming speeds of marine fish in relation to fishing gears. ICES Mar. Sci. Symp., 196:183-189.

Hoar, W.S., and Randall, D.J. 1978. Fish Physiology, Vol. 7. Academic Press, New York. 576pp.

Hutchings, J.A., and Myers, R.A. 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser., 108:21-31.

Kalbfleisch, J.D., and Prentice, R.L. 1980. The Statistical Analysis of Failure Time Data. John Wiley and Sons, Inc., New York. 321pp.

Lee, E.T. 1992. Statistical Methods for Survival Data Analysis, 2nd Edition. John Wiley and Sons, Inc., New York. 482pp.

Lear, W.H. 1984. The winter distribution of cod in NAFO Divisions 2J, 3K, and 3L, based on research vessel catches during 1978-83. NAFO SCR Doc. 84/VI/24, 9 pp.

Main, J., and Sangster, G.I. 1981. A study of the fish capture process in a bottom trawl by direct observations from a towed underwater vehicle. Scott. Fish. Res. Rep., 23:1-23.

Marubini, E., and Valsecchi, M.G. 1995. Analysing Survival Data from Clinical Trials and Observational Studies. John Wiley and Sons, Inc., Chichester. 414pp.

McCallum, B.R., and S.J. Walsh. 1995. Survey trawl standardization used in groundfish surveys. ICES C.M. Doc., No. B:25, 13pp.

Metcalfe, J.D., Arnold, G.P., and Webb, P. 1990. The energetics of migration by selective tidal stream transport: an analysis for plaice tracked in the southern North Sea. J. Mar. Biol. Ass. U.K., 70:149-162.

Muenchow, G. 1986. Ecological use of failure time analysis. Ecology, 67:246-250.

Nelson, J.A., Tang,Y., and Boutilier, R.G. 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations from different environments. Physiol. Zoo., 67:330-354.

Norušis, M.J. 1994. SPSS Advanced Statistics 6.1. SPSS Inc., Chicago. 606pp.

Ona, E., and Godø, O.R. 1990. Fish reaction to trawling noise: the significance for trawl sampling. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 189:159-166.

Parrish, B.B., Blaxter, J.H.S., and Hall, W.B. 1964. Diurnal variations in size composition of trawl catches. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, 155:27-34.

Pitt, T.K. 1969. Migrations of American plaice on the Grand Bank and in St. Mary's Bay, 1954, 1959, and 1961. J. Fish. Res. Bd. Can. 26:1301-1319.

Priede, I.G., and Holliday, F.G.T. 1980. The use of a new tilting tunnel respirometer to investigate some aspects of metabolism and swimming activity of the plaice (*Pleuronectes platessa* L.). J. Exp. Biol., 85:295-309.

Ramm, D.C., and Y. Xiao. 1995. Herding in groundfish and effective pathwidth of trawls. Fish. Res., 24:243-259.

Robertson, J.H.B. 1989. The effect of trawl codend design on selection characteristics. Proc. World Symp. Fish. Gear and Fish. Vessel Design, Nov. 1988, pp. 48-53. Marine Institute, St. John's, Newfoundland, Canada.

Smith, S.J., and Page, F.H. 1996. Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. ICES J. Mar. Sci., 53:597-614.

Soofiani, N.M., and Priede, I.G. 1985. Aerobic metabolic scope and swimming performance in juvenile cod, *Gadus morhua* L. J. Fish Biol. 26:127-138.

Swain, D.P., and Kramer, D.L. 1995. Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada, and its relation to population size. Mar. Ecol. Prog. Ser., 116:11-23.

Taylor, E.B., and McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of Coho salmon, *Oncohynchus kisutch*. Can. J. Fish. Aquat. Sci., 42:2029-2033.

Videler, J.J., and Wardle, C.S. 1978. New kinematic data from high speed cine film recordings of swimming cod (*Gadus morhua*). Neth. J. Zool., 28:465-484.

Videler, J.J., and Wardle, C.S. 1991. Fish swimming stride by stride: speed limits and endurance. Rev. Fish Biol. Fish., 1:23-40.

Videler, J.J. 1993. Fish Swimming. Chapman and Hall, London. 260pp.

Walsh, S.J. 1991. Diel variation in availability and vulnerability of fish to a survey trawl. J. Appl. Ichth., 7:147-159.

Walsh, S.J. 1992. Size-dependent selection at the footgear of a groundfish survey trawl. N. Amer. J. Fish. Mgmt., 12:625-633.

Walsh, S.J. 1996. Assessment of groundfish stocks based on bottom trawl survey results. NAFO Sci. Coun. Studies, 28: 9-24.

Walsh, S.J., and Hickey, W.M. 1993. Behavioural reactions of demersal fish to bottom trawls at various light conditions. ICES Mar. Sci. Symp., 196:68-76.

Walsh, S.J., and McCallum, B.R. 1997. Observations of the varying fishing powers of Canadian survey vessels and trawls. NAFO SCR Doc. 97/66. 10pp.

Walsh, S.J., Millar, R.B., Cooper, C.G., and Hickey, W.M. 1992. Codend selection in American plaice: diamond versus square mesh. Fish. Res. 13:235-254.

Wardle, C.S. 1980. Effects of temperature on the maximum swimming speed of fishes. In: Environmental Physiology of Fishes, pp. 519-531. Ed. by M.A. Ali. Plenum Press, New York.

Wardle, C.S. 1983. Fish reaction to towed fishing gears. In: Experimental Biology at Sea, pp. 167-196. Ed. by A.G. MacDonald and I.G. Priede. Academic Press, London.

Wardle, C.S. 1993. Fish behaviour and fishing gear. In: Behaviour of Teleost Fishes, Second Edition, pp. 609-643. Ed. by T.J. Pitcher. Chapman & Hall, London.

Webb, P.W. 1993. The effect of solid and porous channel walls on steady swimming of steelhead trout *Oncorhynchus mykiss*. J. Exp. Biol. 178:97-108.

Weinberg, K.L., and Munro, P.T. 1997. The effect of artificial light on escapement beneath a survey trawl. ICES C.M. Doc., No. W:07, 15pp.

Winger, P.D., He, P., and Walsh, S.J. 1997. Preliminary analysis of the swimming endurance of Atlantic cod (*Gadus morhua*) and American plaice *(Hippoglossoides platessoides*). ICES C.M. Doc., No. W:13, 16pp.

Wroblewski, J.S., Wade, L.B., and Howse, K.A. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat., Sci., 51:142-150.

Appendices

Appendix One

Summary of the experimental setup for the swimming endurance trials of American plaice and Atlantic cod.

	PLAICE	COD
Swimming Chamber		
length	1.80 m	1.80 m
width	0.50 m	0.50 m
depth	0.46 m	0.26 m
Electricity		
frequency	2 Hz	2 Hz
voltage	8 V	15 V
Lighting		
downstream	3.10 lux	1.44×10^{4} lux
midstream	3.10 lux	1.28×10^{1} lux
upstream	3.10 lux	6.35 lux
Plexiglass Cover	yes	no
Moving Floor Belt	yes	yes
Vertical Black Bars	yes	yes

Appendix Two

Cox proportional hazards model fitted to the swimming endurance data for American plaice.

$$h(t)=[h_0(t)]\ e^{(-0.169\ \cdot\ fishlength\ -\ 0.095\ \cdot\ temperature)}$$

Values of the baseline hazard rates $h_0(t)$ for each of the observed endurance times.

Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$
0.25	1.2537	8.60	90.0781	29.08	304.0505
0.48	2.6074	9.05	94.8894	29.48	314.9677
0.75	4.0574	9.17	99.7469	30.62	326.1164
0.82	5.6144	9.52	104.6510	32.12	337.4027
0.88	7.3032	9.75	109.6369	32.15	349.0589
1.00	9.1047	10.13	114.7505	32.72	361.3843
1.53	12.9199	10.85	119.9972	35.92	374.2811
1.60	14.9900	11.43	125.5819	38.45	387.8855
1.77	17.2081	11.55	131.5548	41.27	402.0898
1.93	19.5060	11.68	137.6787	42.00	416.4910
2.15	21.8614	12.05	143.9096	45.22	431.3188
2.17	24.2786	12.42	150.1970	48.42	446.8622
2.48	26.7927	12.75	156.5226	49.45	462.9109
2.77	29.4022	13.35	162.9990	49.92	479.1874
2.92	32.0706	13.97	169.7124	50.60	496.0479
3.12	34.9036	14.90	176.6102	50.62	513.6440
3.33	37.8964	15.50	183.6390	56.57	532.2207
3.52	41.0077	16.37	190.8500	57.90	552.6841
3.60	44.2946	20.43	198.2239	77.93	575.0512
3.75	47.8270	21.05	205.6699	85.70	599.4123
4.00	51.5736	22.52	213.1888	88.68	625.2279
4.48	55.4382	23.17	220.8187	89.00	651.8482
5.12	59.3979	23.63	228.7539	104.92	679.4771
6.28	63.4276	24.27	245.6754	144.85	707.6435
7.25	67.5964	24.62	254.6110	163.02	739.1602
7.60	71.9268	25.00	263.8606	163.92	775.2763
7.95	76.3509	25.67	273.4455	176.20	813.6595
8.00	80.8250	26.17	283.3409	189.67	854.1715
8.50	85.3831	27.58	293.5036		

Appendix Three

Cox proportional hazards model fitted to the swimming endurance data for Atlantic cod.

$$h(t)=[h_0(t)]\ e^{(0.082\ \cdot\ swimming\ speed)}$$

Values of the baseline hazard rates $h_0(t)$ for each of the observed endurance times.

Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$
0.47	7.390 x 10-7	4.82	8.441 x 10-5	10.23	3.793 x 10-4
0.48	1.504 x 10-6	4.88	8.751 x 10-5	10.37	3.905 x 10-4
0.50	2.296 x 10-6	5.08	9.073 x 10-5	10.60	4.021 x 10-4
0.58	3.117 x 10-6	5.10	9.408 x 10-5	10.90	4.141 x 10-4
0.62	3.970 x 10-6	5.22	9.757 x 10-5	11.10	4.262 x 10-4
0.73	4.846 x 10-6	5.23	1.012 x 10-4	11.27	4.385 x 10-4
0.75	5.738 x 10-6	5.37	1.051 x 10-4	11.42	4.510 x 10-4
0.78	6.645 x 10-6	5.47	1.091 x 10-4	12.60	4.637 x 10-4
0.87	7.570 x 10-6	5.48	1.132 x 10-4	12.73	4.772 x 10-4
1.02	8.511 x 10-6	5.57	1.173 x 10-4	12.92	4.916 x 10-4
1.10	9.470 x 10-6	5.68	1.216 x 10-4	13.07	5.064 x 10-4
1.13	1.045 x 10-5	5.73	1.261 x 10-4	13.12	5.222 x 10-4
1.22	1.146 x 10-5	6.10	1.308 x 10-4	13.40	5.389 x 10-4
1.28	1.251 x 10-5	6.18	1.356 x 10-4	15.07	5.565 x 10-4
1.32	1.360 x 10-5	6.23	1.404 x 10-4	15.25	5.746 x 10-4
1.55	1.471 x 10-5	6.27	1.455 x 10-4	15.43	5.930 x 10-4
1.63	1.584 x 10-5	6.33	1.507 x 10-4	15.78	6.123 x 10-4
1.77	1.821 x 10-5	6.43	1.560 x 10-4	16.03	6.530 x 10-4
1.85	1.946 x 10-5	6.50	1.614 x 10-4	16.23	6.794 x 10-4
1.98	2.076 x 10-5	6.55	1.670 x 10-4	16.32	7.165 x 10-4
2.10	2.212 x 10-5	6.67	1.728 x 10-4	18.18	7.570 x 10-4
2.15	2.495 x 10-5	6.78	1.787 x 10-4	19.75	7.988 x 10-4
2.25	2.642 x 10-5	7.03	1.848 x 10-4	20.83	8.413 x 10-4
2.30	2.797 x 10-5	7.13	1.912 x 10-4	21.12	8.846 x 10-4
2.33	2.964 x 10-5	7.27	1.978 x 10-4	22.03	9.293 x 10-4
2.48	3.144 x 10-5	7.50	2.045 x 10-4	23.93	9.755 x 10-4
2.60	3.332 x 10-5	7.80	2.112 x 10-4	24.42	1.000 x 10-3
2.68	3.712 x 10-5	7.87	2.182 x 10-4	26.17	1.100 x 10-3
2.88	3.905 x 10-5	8.07	2.254 x 10-4	27.38	1.100 x 10-3

Appendix Three continued.

Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$	Time	Baseline Hazard $h_0(t)$
2.90	4.102 x 10-5	8.08	2.329 x 10-4	27.72	1.200 x 10-3
3.22	4.304 x 10-5	8.15	2.405 x 10-4	28.30	1.200 x 10-3
3.78	4.720 x 10-5	8.53	2.484 x 10-4	30.25	1.300 x 10-3
3.82	4.933 x 10-5	8.58	2.566 x 10-4	30.27	1.400 x 10-3
3.88	5.376 x 10-5	8.62	2.649 x 10-4	30.67	1.500 x 10-3
4.02	5.602 x 10-5	8.92	2.732 x 10-4	32.20	1.600 x 10-3
4.20	5.829 x 10-5	9.03	2.906 x 10-4	33.65	1.700 x 10-3
4.42	6.057 x 10-5	9.58	3.090 x 10-4	35.80	1.800 x 10-3
4.57	6.291 x 10-5	9.70	3.185 x 10-4	38.45	2.000 x 10-3
4.65	6.779 x 10-5	9.73	3.280 x 10-4	42.67	2.200 x 10-3
4.67	7.029 x 10-5	9.95	3.378 x 10-4	45.12	2.400 x 10-3
4.68	7.288 x 10-5	10.00	3.478 x 10-4	68.85	2.600 x 10-3
4.70	7.562 x 10-5	10.05	3.580 x 10-4	70.60	2.800 x 10-3
4.72	7.844 x 10-5	10.18	3.685 x 10-4	73.03	3.100 x 10-3
4.78	8.136 x 10-5				